THE UNIVERSITY OF HULL

THE LATE QUATERNARY PALAEOECOLOGICAL HISTORY OF THE GREAT WOLD VALLEY

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by
Mark Bennett Bush, B.Sc.

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SUMMARY

The paucity of polliniferous deposits on the British chalklands has left something of a vaccuum in the known vegetational history of the British Isles. Conflicting ideas of the past landscape of the chalklands have been presented by archaeologists (e.g. Clark, 1936) and botanists (e.g. Tansley, 1939; Pigott and Walters, 1954). The Tansleyan view, i.e. that the chalklands were forested until the Bronze Age, has held sway. Tansley suggested that the dominant species were *Quercus* and *Fraxinus*. This was challenged by the view that *Tilia* may have been a dominant on basic soils (Merton, 1970). Such palaeoecological evidence as exists would suggest that woodlands covered the southern chalklands prior to Bronze Age disturbance, thus vindicating the Tansleyan school.

In this thesis data from a site lying on the Yorkshire Wolds are presented. For the first time a broad spectrum of palaeoecological information is presented from a British Flandrian chalkland deposit. Pollen, bryophytes, plant propagules and macrofossil remains, mollusc and insect data form the basis for an environmental reconstruction of the major water catchment area of the Yorkshire Wolds.

This is complemented by a study of modern analogue sites where a vegetation survey had been undertaken. Plant propagules, molluscs and bryophytes from the surface soil and modern pollen rain (trapped over a one year period) were collected from each site. These data were incorporated into statistical analyses to compare the changes in the fossil data with the range of known

analogue habitats (after Lamb, 1984).

Willow Garth, an ancient carr woodland in the Great Wold Valley, yielded fossil-rich deposits from the late-glacial and Flandrian periods. Although the sedimentary history of this site would appear to be incomplete, an exceptionally detailed image of the palaeoecological history of this valley emerges. The transition from the late-glacial fen and tundra to the Pre-Boreal forest occurred at c. 9200 B.P.. However, the progression towards the mixed woodland of the Boreal forests appears to have been interrupted by the activities of Mesolithic man. It is suggested that Mesolithic hunter-gatherers were 'managing' the woodlands to maximise the carrying capacity of their game. One consequence of this activity was to prevent the forest canopy from closing over the chalk grassland. Calcicolous grassland species were present throughout this period suggesting that the local chalk grassland may never have been totally shaded out. If this was the case the chalk grasslands around the Great Wold Valley would be of considerably greater antiquity than is generally supposed.

During the late-Neolithic and the Bronze Age there is abundant evidence of anthropogenic disturbance with the presence of agricultural weed taxa and pollen of Cerealia. Chalk grassland species are also represented in both the faunal and floral records from this period. Cattle probably grazed the fen and the local wetland flora reached a peak of diversity. In early Saxon times the fen started to dry out and it is suggested that its land use may have changed from a grazed fen to an osier bed at c. 1200 B.P..

I dedicate this thesis to my parents

"Another damned, thick, square book!
Always scribble, scribble, scribble!
Eh! Mr Gibbon"

William Henry, Duke of Gloucester
1743-1805.

"Don't bite my finger -
look where it's pointing"

Warren S. McCullogh
1898 -

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CHAPTER 1: INTRODUCTION

1.1 BACKGROUND AND OBJECTIVES

The chalk grasslands of Britain were once considered, by botanists and archaeologists alike, to have been a natural vegetation community which had existed throughout the post-glacial period. This view was challenged by Tansley (1939) who suggested that the grasslands could not have survived the shading and eventual closure of Boreal forests. He proposed that the most likely dominant of natural chalkland communities would be Fraxinus excelsior (Tansley, 1939). The basic tenets of this hypothesis are that the chalk grasslands are not a climax community, are prone to invasion by shrubs and trees, and can only result from the grazing action of livestock following clearance. Tansley suggested that such clearance first took place in the neolithic period. Hence all chalk grasslands must post-date this period.

In 1954 the debate was re-opened when Pigott and Walters put forward the hypothesis that there had been certain post-glacial refuge areas on the steepest slopes of the chalk. In such areas the soil was considered to have been too thin to have supported tree growth and it was here that the chalk herb flora had survived.

Attempts to assess the ecological antiquity of the southern chalklands of England by palynological methods have been made by Godwin (1962), Thorley (1971) and Waton (1982). Such work however has been largely frustrated by the lack of good palaeoecological records emanating from the chalk (see section

1.2). The results of the above studies have been interpreted to support the view that a closed Boreal forest had existed on the chalk prior to clearance by neolithic and Bronze Age settlers. Evidence from other sources, principally from fossil molluscs, has indicated that the chalk downs were wooded in pre-neolithic times (e.g. Evans, 1971; Kerney et al., 1964).

Previous studies (e.g. Tansley, 1939) have, by implication, treated the northern chalklands as being essentially the same as those of the southern downlands. This has led to generalisations, based on evidence from the southern chalk, being applied to all the British chalkland regions. The assumption that the Downs and the Wolds have had similar ecological histories may prove ill-founded as the northern chalklands are geographically, geologically and climatically distinct. Furthermore, the peoples who settled the north of England were not necessarily the same as those who settled the south and a difference in culture may have been reflected in a difference in their land usage.

Nevertheless, the theories of Tansley have held sway and the current view of the vegetational history of the chalklands may be summarised in the following hypotheses:

i) The chalklands of Britain were forested during the Boreal and Atlantic periods.

ii) The earliest detectable changes in the landscape caused by man were attributable to the neolithic settlers.

iii) The chalk grasslands are anthropogenically induced communities first established by the neolithic graziers.

It is the object of this thesis to investigate the palaeoecology of the Great Wold Valley, a valley which lies in the heart of the Yorkshire Wolds. Particular attention will be paid to the history of the chalk grasslands and where possible the above hypotheses will be tested. To date there has been no satisfactory Late Quaternary palaeoecological record from the northern chalklands.

A further line of investigation will be directed towards establishing the past presence of *Tilia* spp. on the Yorkshire Wolds. In recent years considerable interest has been focussed on the apparent abundance of *Tilia cordata* during the Atlantic and Sub-Boreal period (e.g. Girling and Greig, 1977; Baker *et al*., 1978). This has led some authors to suggest that almost pure *Tilia* forests existed within Yorkshire (e.g. Turner, 1962). Others have suggested that *Tilia* was at least locally dominant (Moore, 1977).

1.2 PREVIOUS PALAEOECOLOGICAL STUDIES RELATING TO THE BRITISH CHALKLANDS

1.2.1 The Pollen Record

Sites located on the chalk where a palynological investigation has been undertaken may be divided into those sites where palaeoecology governed the choice of site location and those where archaeology determined the location. In the former the object has generally been to assess the fossil pollen record of natural peat deposits, whereas in the latter the substrate has usually been a buried soil and palynology has been a useful complement, but secondary, to the main archaeological investigation.

Naturally Occurring Deposits

Natural organic deposits, with the reducing environment essential for pollen preservation, are extremely rare on the chalk. To date only two profiles have been analysed from sites actually on the chalk outcrop, those of Leckford (Seagrief, 1955) and Winchester (Waton, 1982).

Winchester, Hants. (Waton, 1982).

This site, undertaken late in Waton's study of polliniferous deposits in southern England, might have benefitted from a more detailed analysis. The organic deposit, which was located in a valley in the South Downs, had a depth of 4.30 m. Pollen preservation varied throughout the deposit, as did pollen concentration, no absolute methods were used and so the concentration data could not be quantified.

A single radiocarbon date was obtained to date an apparent elm-decline, at 5630 ±90 B.P. (HAR-4342). Nine pollen zones were identified and dates were extrapolated for these; sediment accumulation rates were calculated for 3 phases of sedimentation although Waton recorded 8 stratigraphic boundaries; little weight can be placed on extrapolated dates or sedimentation rates estimated on the strength of a single date.

The lowest zone of the pollen diagram (WT1), attributed to the period *c*. 8670 to 8140 B.P., contained high values of *Corylus*

(31% to 27%) and Quercus (10% to 20%), whilst Betula was only 1% to 2%. The pollen of Chenopodiaceae, Plantago lanceolata and Gramineae (30% to 40%) were present throughout this zone, as were charcoal fragments. In the succeeding zone the occurrence of Betula and Quercus pollen fell, whilst Pinus and Corylus increased; Tilia also increased, Alnus representation rose to a peak, plummetted and then rose again to another peak of 40% of the total pollen count in WT3. Pollen taxa recorded in WT3 included Centaurea nigra, Plantago media/major, Sinapis type and Anthemis type.

Forest disturbance was recorded for the first time in this core in zone WT4, the elm-decline and the first occurrence of Cerealia pollen also occurred within this zone. This was the level dated at 5630 ±90 B.P., an early, but not unlikely, date for the elm-decline. Waton suggested the presence of forest disturbance immediately prior to the elm-decline, coinciding with the first occurrence of cereal pollen. This would agree well with the findings of Scaife (1980) who recorded an identical sequence of events at the fringe of the chalk outcrop on the Isle of Wight. At Winchester these levels were marked by a rise in Plantago lanceolata from 2% to 5% and of Liguliflorae from 3% to 8% of the dry land pollen sum. There was a marked increase in the charcoal content of the basal layer of this zone and pollen abundance was greater than in the previous zones.

The following zone WT5 was essentially similar in character to WT4, except that cereal pollen disappeared until the middle of WT6. This was ascribed by Waton to the late neolithic 'standstill', a period which some authors believe to have been the product of the neolithic culture outstripping its capacity to continue the momentum of development (Bradley, 1978; Whittle, 1980ab).

In the period during WT7 cereal pollen continued to be present but there was an increase in the arboreal pollen component with *Betula*, *Alnus* and *Corylus* totalling 35% of the dry land pollen total. A final clearance phase in early mediaeval times was the last major feature of the pollen diagram.

Some of the most noticeable features of the diagram which Waton did not comment on to any great extent were the apparent sedimentary discontinuities. One was indicated by an inwash layer of chalky clay, coinciding with the wild pattern of the *Alnus* curve in WT3. Several others were suggested by wild fluctuations in the presence of such taxa as *Pinus* and *Dryopteris*, both of which were known for their durability under poor conditions of preservation (Havinga, 1967). Whilst the presence of such discontinuities was not particularly surprising, or indeed worrying, it was somewhat reckless to extrapolate lines of sedimentation accumulation and time across such discontinuities.

Gramineae pollen formed a high percentage of the dry land pollen count (30% to 70%) throughout the diagram and the early occurrence of open ground taxa such as: *Plantago lanceolata*, *P. media/major*, *Centaurea nigra*, Chenopodiaceae and *Sanguisorba minor* were all attributed to plants growing on the river gravels and ground lain open by natural forest fires. The alternative possibility, that of mesolithic forest disturbance, received scant attention.

This was a most promising site and it may still have much to reveal from a more detailed and broader palaeoecological investigation.

Leckford, Hants. (Seagrief, 1955).

This site, which lies well within the chalk outcrop of the South Downs, yielded a 2.10 m core of organic material. It was a great pity that much of this deposit contained little or no pollen. Seagrief recorded the presence of various taxa including the once common agricultural weed Centaurea cyanus, as far as 1.00 m down the core. Between 1.05 - 1.35 m there was a greyish-green mud with shells. The only pollen taxon to be retrieved in any numbers from these levels was Pinus which was interpreted as indicative of Boreal forest conditions. Pollen concentrations were low and selective preservation was a problem which could have accounted for the high proportions of Pinus pollen in sections of this core. The core was undated and the data derived from the pollen analysis too poor to make it worthwhile attempting any reconstruction of the vegetational history of this site.

Peripheral sites

Brook, Kent (Lambert, 1964).

Solifluction sediments near the foot of the North Downs provided the first record of the late-glacial vegetation of south-eastern England. Seven samples were analysed from the lowest 0.25 m of a 3.00 m borehole. A radiocarbon date was obtained for this section of the core indicating an age of 11900 ±160 B.P. (Q-618).

Pollen counts exceeded 100 grains in only 3 of the 7 samples. The overall picture was of an open wetland environment with such herb taxa as Thalictrum, Armeria, Valeriana and Epilobium. Spores of Botrychium, Huperzia selago and Selaginella were also present. The arboreal flora was represented by Betula (undiff.), Pinus, Picea, Juglans, Salix and Juniperus.

The low concentration of pollen in these samples could be attributable to an open landscape in which there was a high bare ground component and low pollen production from a scattered herb community. The low arboreal pollen input during this phase may represent a long distance element. In the samples with the highest pollen concentration Gramineae (62% to 70% of total pollen) and Cyperaceae (17% of total pollen) were the most abundant pollen taxa. In the less well preserved levels the proportions of Gramineae and Cyperaceae changed to 4% and 25% respectively, whilst Betula and Pinus increased to 20% and 45% respectively. This may represent a climatic change and the beginning of the Boreal period, although selective preservation may also be playing a part in the fluctuation of these values.

Many of the remaining sites in this section have been used, either as direct or supporting evidence, to construct arguments supporting the Tansleyan view of chalklands dominated by forests throughout much of the post-glacial. This, however, is a misuse of the data from these sites as none is actually located on the chalk and cannot, therefore, provide evidence regarding the chalklands dissociable from that of their immediate geologies.

Indeed applying the pollen catchment criteria advocated by Jacobson and Bradshaw (1981) these sites would have received less than 10% of their pollen influx from the chalklands.

Wingham and Frogholt, Kent (Godwin, 1962).
Amberley Wild Brooks, Sussex (Godwin, 1943; Thorley, 1971; Waton, 1982).
Lewes, Sussex (Thorley, 1971).
Rimsmoor, Hants (Waton, 1982).
Kingswood, Hants. (Waton, 1982).
Woodhay, Hants. (Waton, 1982)
Snelsmore, Hants. (Waton, 1982).
Litton Down, Dorset (Sidaway, 1963).
Castlethorpe, Lincs. (Preece and Robinson, 1984).

Pollen Diagrams from the Region of the Yorkshire Wolds

The principal relevance of these sites to the current study is in the rate of forest advance, forest composition, and regional climatic conditions during the late- and post-glacial period.

Star Carr, N.Yorks. (Walker and Godwin, 1954).

Star Carr lies in the Vale of Pickering, a broad valley which separates the Yorkshire Wolds from the North York Moors. The pollen record revealed a complete late- and post-glacial stratigraphy, Betula was the dominant arboreal pollen type and the percentage of non-arboreal taxa was low. Although this site is known to have been utilised by Palaeolithic hunters (Clark, 1954) there was no evidence of anthropogenic vegetation disturbance.

The Bog, Roos, Humberside (Beckett, 1975).

The plain of Holderness was formed by a till sheet left by the decaying ice at the end of the Devensian period. The surface of the boulder clay was pocked with meres, one of which was sampled by Beckett. The Bog at Roos has provided the most complete late- and post-glacial pollen record to come from Holderness. Five radiocarbon dates were obtained from the bottom section of the core indicating an age of 13045 ±270 B.P. (BIRM-317) for the basal peats.

The peak of Betula pollen (80% dry land pollen) at 11450 ±230 B.P. (BIRM-407) started to wane and there followed a period when Betula was reduced to 15% to 20% prior to a second major rise which led to a peak of 88% dry land pollen at c. 10200 B.P.. This peak was short-lived as Betula was replaced by Corylus which was consistantly present at 70% to 80% until the rise of Alnus. Pinus had a peak during the cold open period of zone III and a slight resurgence at the end of the period dominated by Betula, but was otherwise of minor importance. Ulmus was first recorded at 10120 ±180 B.P. and thereafter was consistantly present at 5% to 10% of the dry land pollen sum. Quercus peaked slightly later but was of the same order of abundance. Tilia which had arrived at the same time as Alnus reached a peak of 10% of the dry land pollen total before declining synchronously with the Ulmus-decline. The Ulmus-decline was taken to be contemporaneous with one dated at the nearby site of Gransmoor to 5099 ± 50 B.P. (SRR-229) (Beckett, 1975).

Archaeological pollen sources

Many archaeological sites have had some palynological work carried out on buried soils, grain stores and waste pits uncovered during a dig. Often the pollen from such strata was poorly preserved and it was the mollusc remains which provided a better record. Much of the work was reviewed by Dimbleby and Evans (1974). The pollen record from two Wiltshire sites are described here to provide an example of the range of results discovered through these studies.

Avebury, Wilts. (Dimbleby and Evans, 1974)

The most complete biostratigraphy, dating from zone III, was that from the site at Avebury. Pollen concentrations were low and the predominance of fern spores suggested that selective preservation had caused an imbalance in the fossil record. Even in the best preserved layer the pteridophytes accounted for 48% of the pollen and spore sum. Dimbleby and Evans tentatively suggested that there had been a period of forest clearance followed by Corylus and Quercus recolonisation prior to the neolithic period.

Horslip Long Barrow, Wilts. (Dimbleby and Evans, 1974)

Beneath the barrow, which was dated to 5190 ±150 B.P. (BM-180), lay a buried rendzina soil 0.25 m deep. Pollen and molluscs extracted from this deposit indicated that open grassland conditions had existed for some time before the construction of the barrow. Only in the uppermost levels was there any suggestion of woodland encroachment. This was explained as a phase of cultivation giving way to a period of woodland regeneration. Why this should be termed 'regeneration' when there is no evidence for the previous existence of woodland at that site is not made clear in the text.

On the Yorkshire Wolds there have been only two attempts to investigate the pollen content of buried soils. At Rudston the analysis was abandoned due to suspected soil contamination, the result of a previous archaeological dig at the site by the Rev. Greenwell in 1869 (Wiseman, 1972). The other site was Kilham Long Barrow.

Kilham Long Barrow, Humberside. (Evans and Dimbleby, 1976)

This site was situated on the eastern flank of the Yorkshire Wolds, just south of the Great Wold Valley at c. 70 m O.D.. Although the barrow had been constructed during neolithic times (4830 ±125 B.P. (ref. not available)) there was evidence of a mesolithic occupation site underlying the neolithic remains. Pits, hearths and c. 700 worked flints evidenced the presence of mesolithic man at this site.

The buried soil contained Eb and B+ horizons which were silty, chalky loams with a strong humus content. Although no molluscs were preserved in these soils due to the degree of decalcification, pollen was preserved. However pollen was sparse, (< 3500 grains g^{-1}), and counts greater than 160 grains were achieved from only 3 samples. The percentage data could not be taken too literally, especially as the counts contained taxa known to be resistant to decay, e.g. *Tilia*, *Pinus*, Liguliflorae and *Dryopteris* (Havinga, 1967).

In the lowest of three pollen zones identified at 0.16 - 0.20 m the non-arboreal pollen/arboreal pollen ratio was 245%. *Tilia*, with *c*. 5% of the total pollen, was the commonest tree taxon but, overall, Gramineae (60%) was the commonest pollen type. Other taxa represented included *Quercus*, *Pinus*, *Cerealia*, Chenopodiaceae, Liguliflorae, Cyperaceae and Papilionaceae. This zone was suggested as representing an agricultural phase within an open landscape with scattered remnant woodland dominated by *Tilia*.

The middle zone was barren of pollen but the uppermost horizon from 0.12 m to the buried surface was polliniferous. Six samples were counted from this zone, one which again reflected an open environment with arable agriculture. The arboreal representation was increased with the presence of: *Alnus*, *Pinus*, *Quercus*, *Tilia* and *Ulmus*. *Tilia* was the most abundant arboreal pollen taxon with *Corylus* as the most abundant shrub. *Cerealia*, *Plantago lanceolata*, *P. coronopus*, Chenopodiaceae and Liguliflorae were consistently present and the most abundant pollen type was that of Gramineae with up to 50% of a count of

380 dry land pollen.

Evans and Dimbleby (1976) suggested that this sequence represented two phases of agriculture with a period in between when the soil was not disturbed, during which time a sol lessivé was formed.

Although Tilia was the dominant tree pollen in these samples it does not necessarily follow that it was the dominant tree on the Yorkshire Wolds at this time. Tilia pollen is known to be resistant to decay and the values might be artificially inflated through selective preservation.

The most striking result of this analysis was the suggestion of an early date for agriculture. There had been either a period of deforestation by mesolithic or very early neolithic cultivators on the wolds, or the wolds had never been forested.

1.2.2 Plant Macrofossil Assemblages

Macrofossil remains of plants were used for environmental analyses before the upsurge of interest in pollen analysis. There followed a period in which little progressive work was done using macrofossils. In England there has still been little work, outside of an archaeological context, directly aimed at environmental analysis using plant macrofossils from chalkland deposits. At Wingham and Frogholt (Godwin, 1962) the macrofossils revealed a rich local fen flora but there was no quantitative analysis. The mollusc fauna analysis of solifluction lobes in the South Downs by Kerney et al. (1964) also produced a list of late-glacial seeds for Brook in Kent, but again there was no attempt to establish statistically significant data.

Brook, Kent (Lambert, 1964).

The presence of fruits of *Arctostaphylos urva-ursi*, *Betula nana* and *Salix herbacea* indicated a heathland element which was widespread in late-glacial times. *Pedicularis palustris*, *Menyanthes* and *Carex* spp. suggested the presence of a fen. The presence of pools with still or slow moving water was provided by the pollen of *Potamogeton* and *Sparganium*/*Typha angustifolium* and the fruits of *Schoenoplectus*.

1.2.3 Bryophytes

As with other plant macrofossils there has been little work aimed specifically towards bryophyte assemblages on the chalk. Dickson (1973) lists many of the significant finds such as the mosses in the Dimlington silts, laid down *c*. 18500 B.P., which were all of one species: *Pohlia wahlenbergii* var. *gracilis* (Penny *et al*., 1969).

The majority of bryophyte finds were associated with archaeological deposits such as the Brigg dugout, which dated to 2784 ±100 B.P. (Q-78), from which 22 species of moss were recovered (Smith, 1958). These had been used to caulk the seams of the stern board and to make a patch. All but one species, *Distichum capillaceum*, were characteristic of moist shaded river banks. However the location of the river bank is unknown, as the mosses could have been collected along any of the routes of these Bronze Age traders.

Other archaeological work included the analyses of the bryophytes from Silbury Hill, Avebury by Williams (1976). 8 moss species were recorded, including *Pseudoscleropodium purum*, from stacked turves cut at the time of the barrow construction. *P. purum* was the most abundant of the mosses in the deposit and was found to be one of the dominant bryophytes of chalk grassland in modern assemblages (Cornish, 1954; Hope-Simpson, 1941a). The other taxa found in the turves have all been recorded from chalk grassland. It was apparent that these turves had been cut from an area of chalk grassland which was in existence at the time of the construction of the mound at *c.* 4095 B.P..

Bryophytes from meres and fens have been recorded frequently during the stratigraphical description of a sediment, or from a quick inspection for obvious macrofossils. This inevitably biased the data in favour of the larger species and provided data which were not necessarily valid for any detailed interpretation.

At Aby Grange Suggate and West (1959) recorded 10 bryophyte taxa; amongst the species recorded from the late-glacial were: *Calliergon giganteum*, *Drepanocladus revolvens*, *Mnium punctatum*, *Polytrichum alpinum* and *Scorpidium scorpioides*. Beckett (1975) recorded *Sphagnum* sp., *Polytrichum* sp. and *Fontinalis antipyretica*, from the Bog at Roos, Humberside.

1.2.4 Mollusc Remains

As molluscs are poorly preserved under acidic groundwater conditions, records of the mollusc fauna are rare from polliniferous deposits. The deposits which do contain fossil molluscs are generally those of solifluction deposits in chalk valleys, or from buried soils beneath earthworks on the chalk.

Mollusc Records from Natural Deposits

Brook, Kent (Kerney *et al*., 1964).

From a series of sites in small valleys along the escarpment of the Kentish chalk Kerney *et al*. revealed a detailed molluscan history of the North Downs. Species such as *Lymnaea truncatula*, *Anisus leucostoma*, *Vallonia pulchella* and *Pupilla muscorum*, were abundant in an open, marshy landscape during the late-glacial. The presence of truly aquatic species suggested the presence of pools of open water.

With the climatic amelioration there arrived a fauna characteristic of temperate woodlands e.g. *Acicula fusca*, *Cochlicopa* spp., *Lauria cylindracea* and *Acanthinula aculeata*. A marked decline in these species and an increase in such taxa as *Vallonia excentrica*, *Pupilla muscorum* and *Vertigo pygmaea* indicated a return to open conditions which was interpreted as a zone VIIb/VIII clearance.

Utilising the pollen, propagules and mollusc data from these sites Kerney *et al*. concluded that the late-glacial vegetation of the southern chalklands could be summarised as:

> "Wide expanses of marshy ground mantled by herbaceous vegetation and bearing scattered birch trees, interspersed with swamps and shallow pools."
>
> (Kerney *et al*., 1964, p.185)

The record from this site indicated that the Boreal and Atlantic periods were ones when a shaded environment predominated. Unfortunately the molluscs do not yield any information as to which trees were present, and there was no botanical evidence from this site after the late-glacial. Evidence of temporary forest clearance and subsequent regeneration was evident at the Rifle Butts section at Brook. Kerney _et al._ (1964) suggested that this may have been contemporaneous with the woodland disturbance recorded by Godwin (1962) at Wingham and Frogholt. However, further work at the Rifle Butts section of the Devil's Kneadingtrough established a date of 4540 ±105 B.P. (BM-254) for the main clearance phase (Burleigh and Kerney, 1982). This was considerably earlier than the Bronze Age/Iron Age date suggested by Godwin.

At another site, a little further down the valley from the Rifle Butts section, Kerney _et al._ (1964) recorded evidence of a clearance phase associated with some fragments of neolithic Beaker-Ware. This corresponded well with the dated clearance horizon from the Rifle Butts.

Folkestone and Holborough, Kent (Kerney, 1963).

A molluscan fauna which suggested fluctuating environmental conditions was obtained from this site on the South Downs. The deposits were composed of stratified chalk muds and rubbles dated to _c._ 13950 - 10250 B.P. and a separating band of rendzina dated to 11950 - 10750 B.P.. The deposits were ascribed to the Allerod period and the zonation of the mollusc faunas followed that of a 'normal' zone I - III pollen zonation as recorded at other sites in eastern England.

Ancholme Valley, Brigg, Lincs. (Preece and Robinson, 1984).

The tributary valleys of the Ancholme Valley provided a number of sites where tufaceous deposits had formed at the base of valley slopes. These deposits were analysed for their mollusc and ostracod contents. The samples were found to represent two phases of deposition. One, from near Brigg, represented the late-glacial period and another from Castlethorpe provided samples dated to 3410 ±80 B.P. (BM-1795).

The late-glacial fauna included the boreo-alpine species: *Vertigo genesii*, *Catinella arenaria* and *Columella columella*. These species have a modern distribution confined to northern Scandinavia and scattered locations in the Alps (Kerney and Cameron, 1979). There were also the aquatic species *Lymnaea* spp., *Anisus leucostoma* and cf. *Oxyloma pfeifferi*, which all have modern holarctic distributions.

At Castlethorpe, the richest of the sites in terms of species diversity and shell concentrations, there was evidence to suggest that there had been a succession of habitats from fen pools early in the Flandrian towards a later, more wooded phase. This later phase was indicated by an increase in shade-loving species such as *Discus rotundatus* (10%), *Spermodea lamellata* and *Acicula fusca*. There then followed a decrease in these forest taxa and a recovery by open ground species such as *Vallonia excentrica*, *Vertigo pygmaea* and *Pupilla muscorum*. These suggested the return of an open ground environment and were interpreted as indicating a phase of Bronze Age clearance. It was from this level that the date of 3410 ±80 B.P. was obtained.

Molluscs from Archaeological Sites

The sites surveyed by Dimbleby and Evans (1974) for fossil pollen had been the subject of previous research for their mollusc record by Evans (1972). Examples of the mollusc records are presented from the same sites as those selected as examples of the pollen record from these deposits.

Avebury, Wilts. (Evans, 1972).

Soil bured beneath a neolithic henge contained five mollusc assemblage zones, the oldest dating from the late-glacial. In this zone open ground species tolerant of tundra conditions predominated. Towards the end of the zone there was an increase in the species of open woodland habitats such as: Discus rotundatus, Carychium tridentatum and assorted Zonitidae.

The woodland molluscs dominated the assemblages in the basal portion of the diagram until there was a peak of Pomatias elegans, an indicator of disturbed ground. As this was followed immediately by an increase in species of open ground habitats, e.g. Vallonia spp. and Helicella itala, this was suggested to be a phase of anthropogenic woodland clearance.

Horslip, Wilts. (Evans, 1972).

An antler found in the earth disturbed by the construction of the Long Barrow was dated to 5190 ±150 B.P. (BM-180) (Ashbee and Smith, 1966). The site lay 1.7 km west-north-west of Avebury and yet the image of the local vegetation obtained from the mollusc record from Horslip was quite different from that found at Avebury.

All the molluscs recovered from the soils buried beneath the Horslip barrow suggested that there had been very little forest cover at this site (Connah and McMillan, 1964). Open ground taxa, e.g. Vallonia costata, Helicella itala and Pupilla muscorum, accounted for 42% of the molluscs identified. Connah and McMillan (1964) suggested that the habitat had been open downland with occasional patches of scrub.

The pattern of the mollusc record from Avebury was repeated at numerous sites. The general trend was to suggest a degree of forest cover prior to a neolithic clearance. However, even during periods when woodland faunas predominated, the molluscs generally associated with open ground habitats were seldom completely absent and at some sites, e.g. Horslip, they were never seriously reduced by the shade tolerant species.

1.3 SUMMARY OF RESEARCH AND FORMULATION OF A BASIC METHODOLOGY

Existing evidence regarding the vegetational history of the chalklands is inconclusive and inconsistent due to the lack of corroborative pollen or macrofossil data. Previous research on the chalklands has been hampered by the lack of deposits where plant or insect remains might have fossilised. The only site, Winchester, which might have yielded a long and detailed fossil record from the southern chalk was only investigated for its pollen record. Chalkland sites with good conditions for micro- and macrofossil preservation are a true rarity and when found their potential must be recognised and exploited.

Detailed studies, making use of as wide a variety of techniques as possible, have been advocated by West (1970). Although the broad vegetational history of much of Britain has been very fully recorded there have been few attempts to reconstruct individual ecosystems in any detail. It is only through a multi-faceted study that the continuity of these relationships can be investigated.

In this study it was decided to gather data from a wide variety of plant and animal remains. Sediment cores were sought from which fossil pollen, plant propagules, bryophytes, other plant macrofossils, molluscs and insects could be extracted. The data from these assemblages were synthesised to form the first broad palaeoecological study from the British chalklands. The reconstruction of past communities was enhanced by comparison with pollen, propagule, mollusc, bryophyte and vegetation data from a range of modern analogue sites. These data were also utilised in R-rel (Andersen, 1973) and multivariate analyses (after Lamb, 1984), and a comparison made of the applicability of these latter techniques.

CHAPTER 2: THE STUDY AREA

2.1 THE ENVIRONMENTAL SETTING

2.1.1 Location, Geology and Topography

The Yorkshire Wolds are the northernmost major chalk outcrop in Britain. Extending in an arc from the Humber to Flamborough Head they cover an area of 480 km^2 (Fig. 2.1). At Sewerby the chalk disappears beneath the drift deposits from the last glaciation.

The chalk, which is of Upper Cretaceous age, lies unconformably on the lower Cretaceous, primarily the Albian, and the Jurassic. The chalk oversteps these to a varying extent and there may be a variety of underlying rock types from the Lower Lias to the Speeton Clay. The depth of the chalk increases southwards and inland; at the Tyne Fault Hole the depth of chalk is 265 m. At Flamborough Head the depth of the chalk is 320 m and further inland it reaches a maximum of 420 m (Neale, 1974).

For many years it was assumed that the British chalks were relatively homogeneous and were divided into the Upper, Middle and Lower chalk. This system was first developed to explain the structure of the chalk in France and was found to be applicable to the southern chalks of England. Recent work by Wood and Smith (1978) suggests that a different nomenclature should be used for the chalk of the Lincolnshire and Yorkshire Wolds. They suggest that the northern chalk was deposited at a different time from the southern chalks and indeed shows a greater fossil faunal affinity to the chalks of Germany, Poland and the U.S.S.R., than to the chalks of southern England. If this is true it explains

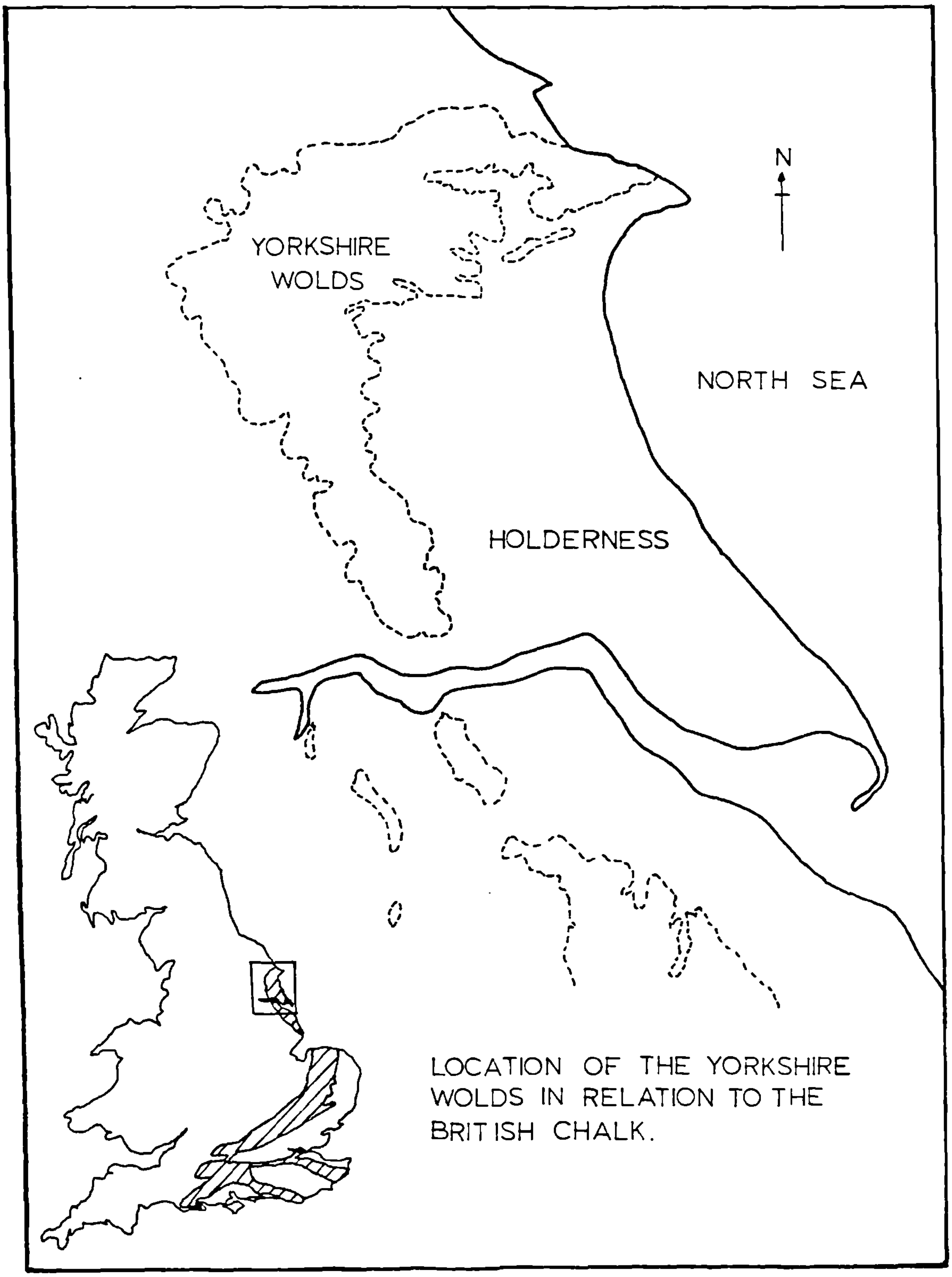


FIG. 2.1: THE LOCATION OF THE YORKSHIRE WOLDS IN RELATION TO OTHER AREAS OF BRITISH CHALK.

why the chalks of northern England have different properties from those of the south. Wolds chalk is harder, with a greater number of marl bands and a zonation and distribution of flints (Wright and Wright, 1942) different from the chalks of the south. Based on these marl bands Wood and Smith (1978) divide the Wolds chalk into not three but four zones of deposition: the Flamborough, Burnham, Welton and Ferriby.

The northern and western flanks of the Wolds are scarp slopes rising from the vales of Pickering and York, respectively. There is a broad regional dip to the south-east where the Wolds are overlain by the Pleistocene and more recent deposits of Holderness.

Contours at the base of the chalk reveal a surface dipping east to north-east in the southern part of the Wolds. Further to the north the chalk forms a dog's leg as it turns eastwards to form the northern arc of the Wolds. The chalk reaches the coast at Flamborough Head where it forms a spectacular cliffed coastline from Bempton south to Bridlington. As the chalk swings eastwards, so the direction of the dip changes from west to east, through to north-west to south-east.

The overall appearance of the Yorkshire Wolds is much smoother, because of past glacial activity, than that of the North and South Downs, with gentler gradients on both the scarp and dip-slopes. The Wolds are deeply dissected by dry valleys, fossils of a period of strong fluvial erosion.

2.1.2 Glacial History and Superficial Deposits

It is widely held that the Wolds were not extensively glaciated during the Devensian period. Indeed the last glaciation of the Wolds may have been pre-Wolstonian (Catt, 1978, 1981; Straw, 1979a,b). There is some evidence to suggest that ice tongues extended up the northern and eastern edges of the Wolds and even that ice overtopped the interfluves along the Great Wold Valley. Evidence for this may be seen in the quantities of erratic stones in the fields around the Great Wold Valley.
The pre- and early Devensian soils of the Yorkshire Wolds were probably remanie stones on bare chalk following the weathering and erosion of previous drift deposits during the Ipswichian Interglacial (Catt et al., 1974). The last glacial phase of the Devensian culminated in an ice advance at approximately 18000 B.P. (Penny et al., 1969). The ice-sheet advanced across the North Sea Basin, which was dry due to the glacio-eustatic lowering of the sea level, but stopped at the foot of the chalk outcrop. To the north and west other ice sheets approached the Wolds, but it is thought none overran the highest portions of the chalk. Although not covered by ice the Wolds were a glacial foreland subject to periglacial conditions. Evidence of this may be seen in such features as the small scale patterned ground at Wharram Percy (Ellis, 1981) and the large scale patterned gound in the southern part of the Wolds (Evans, 1976; Williams, 1964). During the advance of the eastern ice sheet, outwash gave rise to morainic deposits which were of finely crushed rock and sand. These deposits were eroded by the periglacial winds and deposited in a relatively even layer across the Wolds (Catt, 1978). These

loessic soils were almost certainly deposited over a widespread area but they have only remained in situ where they overlie calcium carbonate rich rocks. This is due to the stabilisation of the loess by secondary $Ca\ CO_3$ cementation during phases of erosion (Catt, 1978). The loess deposit was eroded from the steeper slopes of the Wolds, but provided the basis for a fertile soil on many of the more gentle slopes and in the valley bottoms. Without the loess the Wolds soils would have no mineral material other than calcium carbonate for soil formation and thin organic rendzinas, poor in trace elements would prevail (Catt, 1978).

Material eroded from the steeper slopes prior to soil formation was moved downslope into hollows and to the floors and lower slopes of valleys to form chalky head or coombe deposits (Catt *et al*., 1974).

There are no dates available for the end of the glacial phase from sites actually on the Wolds, due to the lack of palaeoenvironmental work carried out in this region. There are, however, several dates for deglaciation from the Vale of York, Holderness and the North York Moors. Jones and Gaunt (1976) obtained a date of 10469 ±60 B.P. (SRR-870) from a peat at Cawood near Selby. Pollen evidence from two samples within this deposit are comparable with pollen zone III assemblages obtained by Bartley at Tadcaster (Bartley, 1962).

An approximate date for the glacial maximum of *c.* 18240 ±240 B.P. (Birm. 108) in north-eastern England was provided by Penny *et al*. (1969). This was based on the dating of a band of moss and silts lying beneath the Drab till at Dimlington on the Holderness coast. The till reaches its southern limit within 15 km of this site leading Penny to suggest that the Dimlington silts were covered by till shortly before the end of the glacial expansion and therefore provide an approximate date for the Devensian glacial maximum in Holderness.

Jones (1977) suggested that within 2000 years of this glacial maximum, ice-sheets lying on the North York Moors had begun to fragment and the separated and stagnating ice in the valley bottoms had started to decay. This hypothesis was based on the dating of a rich assemblage of fenland mosses in silts between solifluction deposits at Kildale Hall, N. Yorks. The mosses were dated to 16713 ±340 B.P. (SRR-145) (Jones, 1977).

Other deposits on or near the North York Moors which have yielded dates which can be correlated to pollen profiles have been: Neasham which provided a date of 11561 ±250 B.P. (no ref. given) for middle pollen zone II (Blackburn, 1952), Flixton where a date of 10413 ±210 B.P. (no ref. given) was obtained for a late zone II or early zone III sample (Walker and Godwin, 1954) and from Seamer Carrs where the date for early zone II was 13042 ±140 B.P. (Jones, 1976).

Further evidence from the region comes from The Bog at Roos where Beckett (1975) found pollen and organic deposition to start at c. 13045 ±270 B.P. (Birm-317). These deposits were attributed to pollen zone I (after Godwin, 1940).

During the Loch Lomond readvance of c. 10500 B.P. there was considerable solifluction activity resulting in the deposition of tufas on the North and South Downs (Kerney et al., 1964) and on the Lincolnshire Wolds (Preece and Robinson, 1984). Deposits of cover sand with depths of up to 7 m have been recorded from the

Lincolnshire Wolds and the Vale of York (Buckland, 1984). The dating of sediments underlying and overlying these sands suggested that the time of deposition was c. 10700 - 10400 B.P.. Buckland suggested that these sands were eroded from tills lying to the west of the Lincolnshire Wolds and were a product of aeolian deposition (Buckland, 1984).

In brief it may be seen from this evidence that the glacial maximum of c. 18200 B.P. was a relatively short lived period, coming right at the end of the Devensian period. Furthermore, there is some evidence for glacial retreat, or at least of ice stagnation, at c. 16000 B.P. and widespread evidence of a general climatic amelioration prior to 13000 B.P..

2.1.3 Climate

The present climate of the Yorkshire Wolds is cool temperate with July mean daily maxima of c. 19°C (Tout, 1976) and a mean annual rainfall of c. 600 - 800 mm (Atkinson and Smith, 1976). Thus the Yorkshire Wolds are slightly cooler and drier than the southern chalklands which have mean July daily maxima of c. 21°C (Tout, 1976) and a mean annual rainfall of c. 800 mm (Atkinson and Smith, 1976). Tout (1976) also records that the mean daily April maximum temperature for the Yorkshire Wolds is 6°C, whereas that of the southern chalklands is up to 2°C warmer. This suggests that there might be an earlier start to the growing season in the south.

2.2 THE STUDY SITE

2.2.1 Site Selection, Location and Description

Berglund (1979) suggested that the optimal site characteristics for the determination of regional vegetation and climatic changes through pollen analysis would be a lake of 25 - 50 ha in which there was an annual deposition of 0.5 - 1 mm of sediment. In such a lake 70% of the pollen influx might be expected to have been derived from a distance of more than several hundred metres (Jacobson and Bradshaw, 1981). If there had been such a lake on the English chalk it would probably have been sampled in the great expansion of palynological investigations in the 1950's and 1960's. That no such site existed has meant that palynologists have had to search for alternative depositional environments.

In general archaeological deposits, e.g. buried soils, have proved unsatisfactory for pollen analysis where they overlie a chalk substrate. Of the natural deposits sampled on the chalk only the late-glacial solifluction deposits at Kent and the site at Winchester have come close to providing a reliable image of the past vegetation of this geology.

The main reasons for the scarcity of sites with edaphic conditions suitable for pollen preservation on the chalk are the low rainfall in chalkland areas and high permeability of the soil and bedrock which seldom, if ever, allow permanent pools to lie on the chalk itself. So far, a polliniferous deposit in a solution hollow, or a doline, which would be the best sites one could reasonably hope for on the chalk, has not been found.

Valley sediments are the only deposits located, to date, which are close enough to the chalk to yield information on the past vegetation of that substratum. Valley fens will usually be either spring or river fed. Spring fed fens are common along the backslopes of the chalk but the springs are prone to be seasonal; when flowing they may rework the sediment and usually they cannot support any significant depth of peat formation.

The problems presented by a stream fed fen are peat erosion by the stream wandering within its valley during the post-glacial period, reworking of material from higher in the catchment and an inwash of pollen from other geologies unless the stream drains only from the chalk.

To go about finding likely sedimentary deposits on the Yorkshire Wolds, Ordnance Survey maps and local floral maps (Crackles, 1973) were consulted. Many sites were visited but the deposits were found to be less than 0.5 m deep. Samples obtained from buried soils and sedimentary deposits of 0.5 m or more were analysed for their fossil pollen content.

Archaeological deposits

Bronze Age buried soils were obtained from archaeological digs taking place from Fimber, Burythorpe and from two sites at Thwing. The deposits from these sites contained few grains of pollen, all of which were Liguliflorae (Taraxacum type), Pinus or Gramineae. The pollen in these samples appeared to have suffered considerable selective preservation and so the analyses were not pursued.

Deposits from a saxon/mediaeval dam at Wharram Percy were analysed because of the archaeological interest of this site. A detailed pollen diagram from the late-saxon period was obtained (Appendix 2).

Natural deposits

None of the spring fed fens sampled had more than 0.3 m of organic deposit. Some ponds on the tops of the wolds, shown on Ordnance Survey maps, without exception proved to be dew-ponds probably dating to the period of enclosures. These and the village ponds of such ancient villages as Wetwang were cleaned out regularly and so had little to offer the palaeoenvironmentalist.

The Great Wold Valley was investigated and here four potential sites were identified.

i) Fishponds Wood, as the name suggested, had been disturbed for the construction of fishponds. In the undisturbed areas the organic sediment did not exceed 0.5 m.

ii) Caythorpe Wood was an alder carr woodland beside the Gypsey Race stream. Although there was a 0.6 m deposit of waterlogged peat on the woodland floor the entire deposit was corrugated by the marks of ridge and furrow cultivation. The fibrous nature of the peat and the clear signs of disturbance argued against any great antiquity in this deposit and so samples were not analysed from this site.

iii) Thorpe Marsh, lying 0.5 km upstream of Caythorpe Wood, was an expanse of wetland which had been recently disturbed for the creation of a private nature reserve. In the undisturbed areas 0.54 m of silty clay was found to underlie 0.15 m of organic material. The clay was well sorted and contained many mollusc shells and shell fragments. There were also occasional flints. An aquatic environment was suggested by the molluscs present, e.g. *Anisus leucostoma*, Succinidae, Lymnaidae, *Planorbarius corneus*, *Bithynia tentaculata* and *Pisidium* spp.. Only a few specimens representing a terrestrial, possibly a grassland environment, were observed, e.g. *Aegopinella nitidula*, *Cochlicopa lubrica*, *Vallonia excentrica* and *Trichia hispida*.

The deposit contained no plant propagules or recogniseable macrofossils and was barren of pollen. As the predominantly wetland mollusc assemblage was going to be of little value in isolation the analysis was not pursued.

iv) Willow Garth, a 'closed' Yorkshire Wildlife Trust nature reserve, was a valley alderwood which provided a 0.96 m core of gyttja and peat during the initial site survey. This was analysed and found to be polleniferous throughout its length. The basal portion of this core was ^{14}C dated at 8160 ±150 B.P. (HAR-5064). The site was revisited and a full programme of stratigraphic and topographic surveying undertaken. The deepest core obtained was 1.18 m in depth. Samples from this spot were extracted for micro- and macrofossil analysis, radiocarbon dating and pH and organic carbon content analysis.

After an extensive search I believe Willow Garth to be the only site on the Yorkshire Wolds to offer a palaeoecological record of much of the late- and post-glacial period. It was decided therefore to study this one site in great detail, rather than to extend the study to include peripheral sites as had been done by previous workers when confronted by a lack of further sites in the preferred area.

2.2.2 Willow Garth: Location

Willow Garth (Ordnance Survey grid ref. TA 126676) lies in the Great Wold Valley in the Yorkshire Wolds (Fig. 2.2). The Great Wold Valley, which follows the line of the Hunmanby Fault, has many tributary valleys draining the north-eastern portion of the Yorkshire Wolds. For the most part these valleys are dry, but some have springs the water of which, if not absorbed back into the permeable soils, flows into the Gypsey Race. The Gypsey Race, the largest stream flowing on the Wolds today, rises near the western edge of the Wolds at Wharram-le-Street and flows on the surface as far as Boynthorpe where it is absorbed into the gravels of the valley floor. After flowing underground for 15 km the stream reappears at Rudston. Seasonal water-table fluctuations cause the Gypsey Race to alter not only in discharge but also in length. Strickland (1812) recorded that in wet winters the Gypsey Race rose 1.5 km downstream of Boynton (i.e. c. 2 km upstream of the usual position).

The Gypsey Race is now an underfit stream. It is generally about 5 - 10 m across, flowing in a valley which at Willow Garth is c. 450 m wide and at about 18 m O.D. elevation. In the lower reaches of the Great Wold Valley the meanders of the Gypsey Race have a wavelength as great as 1560 m Lewin (1969). The flow required to form such meanders would be c. 700 m^3 sec^{-1} (Lewin, 1969). This is considerably greater than the flow recorded by Lewin of 28.3 m^3 sec^{-1}. Local farmers told me of how the Gypsey Race would overtop its banks in winter and flood much of the valley bottom, with the water ponding on Willow Garth. This has not been observed in recent years, possibly due

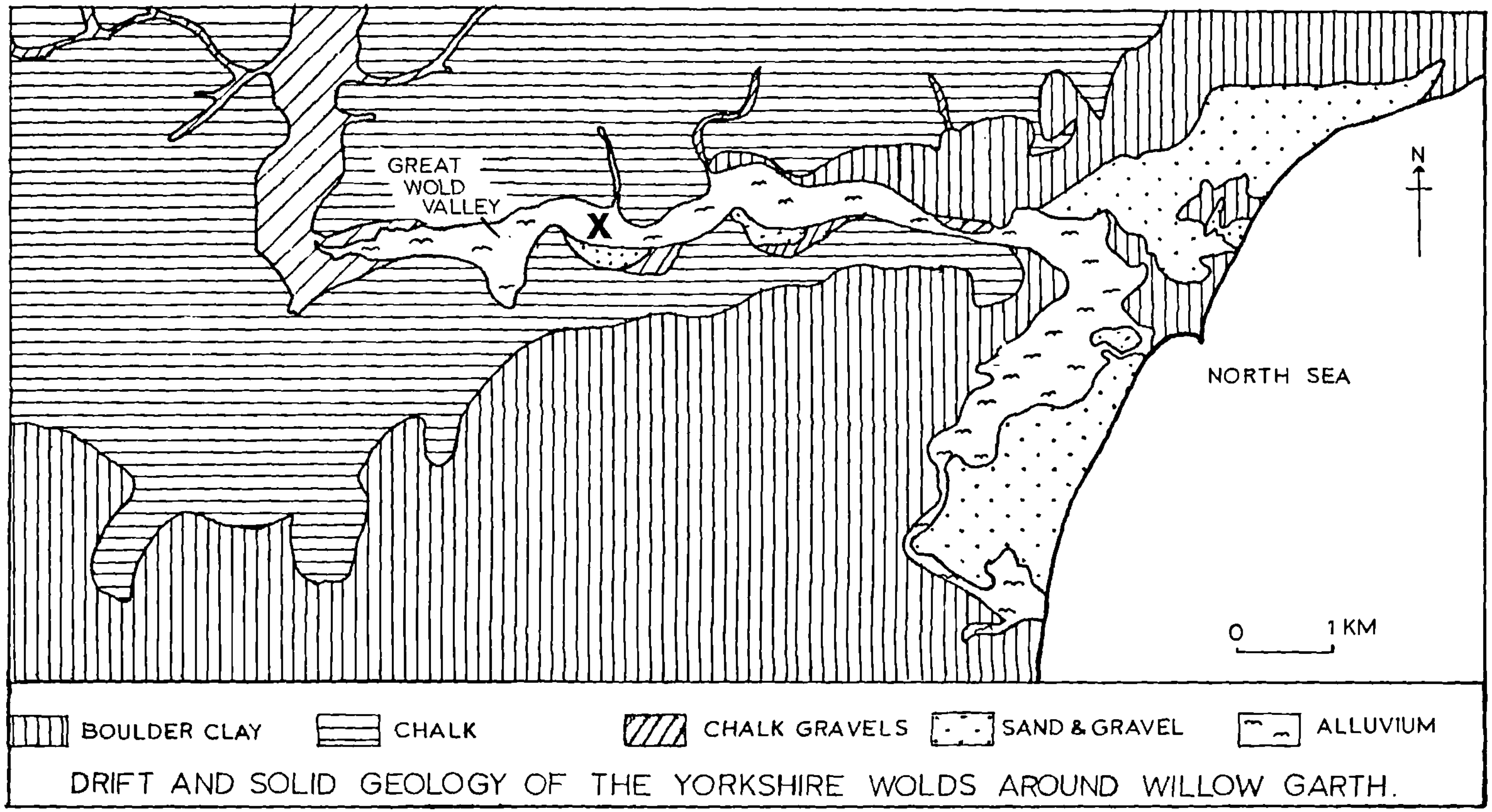


Fig. 2.2. The drift and solid geology of the Yorkshire Wolds around Willow Garth. Taken from the one inch ordnance survey sheet. 'x' marks the site of Willow Garth.

to water extraction for agriculture, and deep land drainage.

Immediately upstream of Willow Garth the Great Wold Valley is constricted from being c. 450 m across to being less than 120 m wide. The valley floor is not flat, as might be expected in a valley containing a meandering stream, but has a gently shelving floor covered in large hummocks of sandy material. When the soil has been freshly ploughed sandy patches are visible, as are occasional patches of darker organic-rich soil. The sudden constriction of the valley above Willow Garth is caused by a moraine deposit on the southern side of the valley. This deposit is not marked on the drift diagram (Fig. 2.2) as the deposit is so thin it may not have been considered a major till deposit by the Ordnance Survey. The extent of the till sheet is not known, although a rough survey of the local fields showed that there were considerable numbers of erratic pebbles even on the highest points for 1 km west along the ridge which forms the southern interfluve of the Great Wold Valley near Willow Garth. This could suggest that an ice-tongue reached up the Great Wold Valley and was of sufficient depth to cover the highest ground (c. 84m O.D. elevation) to the south. Alternatively, the ice may have lapped up over the gentle backslope of the Wolds from Holderness and reached the crest of the southern watershed without entering the valley below. This advance was possibly the one documented by Penny et al. (1969) at Dimlington and therefore could have occurred at c. 18000 B.P..

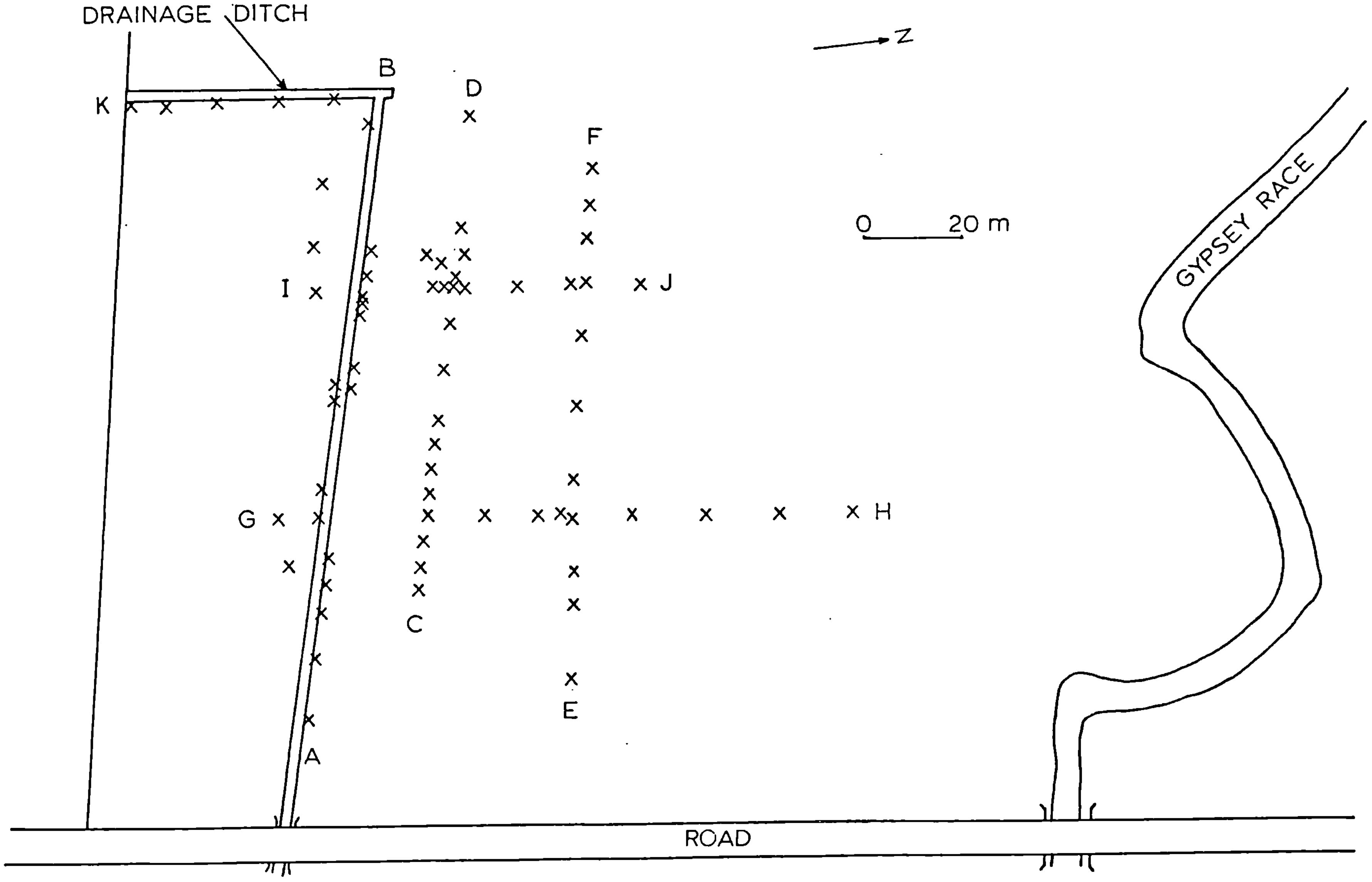
2.2.3 Willow Garth: Stratigraphy

Data for the stratigraphic survey were obtained from 63 bore-holes (Fig. 2.3). In addition to these the upper 0.0 - 1 m of stratigraphy was revealed in the faces of two drainage ditches (Fig. 2.3).

In one of these drainage ditches, there is a section through a sandy hummock on the south-western corner of Willow Garth. The exposure revealed orange-brown sands which formed the bulk of the 2 m high hummock. Small flint fragments (<5 cm) and other chips of stone lie within the sandy matrix; a particle size and stone orientation analysis of these deposits is currently being undertaken by Dr S. Ellis. This hummock appeared to be of a coarser texture (predominantly fine sand and medium sand - c. 60 to 600 μm) and contains less silt, than the loessic deposits found on much of the Wolds (S.Ellis pers comm). Although the exact origin and date of deposition of these sediments remains unclear, it is possible that they are late-glacial aeolian features. This does not conflict with the presence of small stones (<2 cm), which might suggest water rather than wind as the transporting agent, since these have been recorded in periglacial aeolian deposits elsewhere (Washburn, 1979).

However the presence of material up to 5 cm in size suggests that the hummocks are also derived, at least in part, from material which has moved downslope by solifluction, soil creep or surface wash, coming to rest at the break of slope in the valley bottom. If this is the case, the apparent absence of mollusc or other organic remains suggests that downslope movement occurred soon after the initial deposition of the sands under

FIG. 2.3 : LOCATION OF BOREHOLES AND TRANSECT LINES AT WILLOW GARTH.



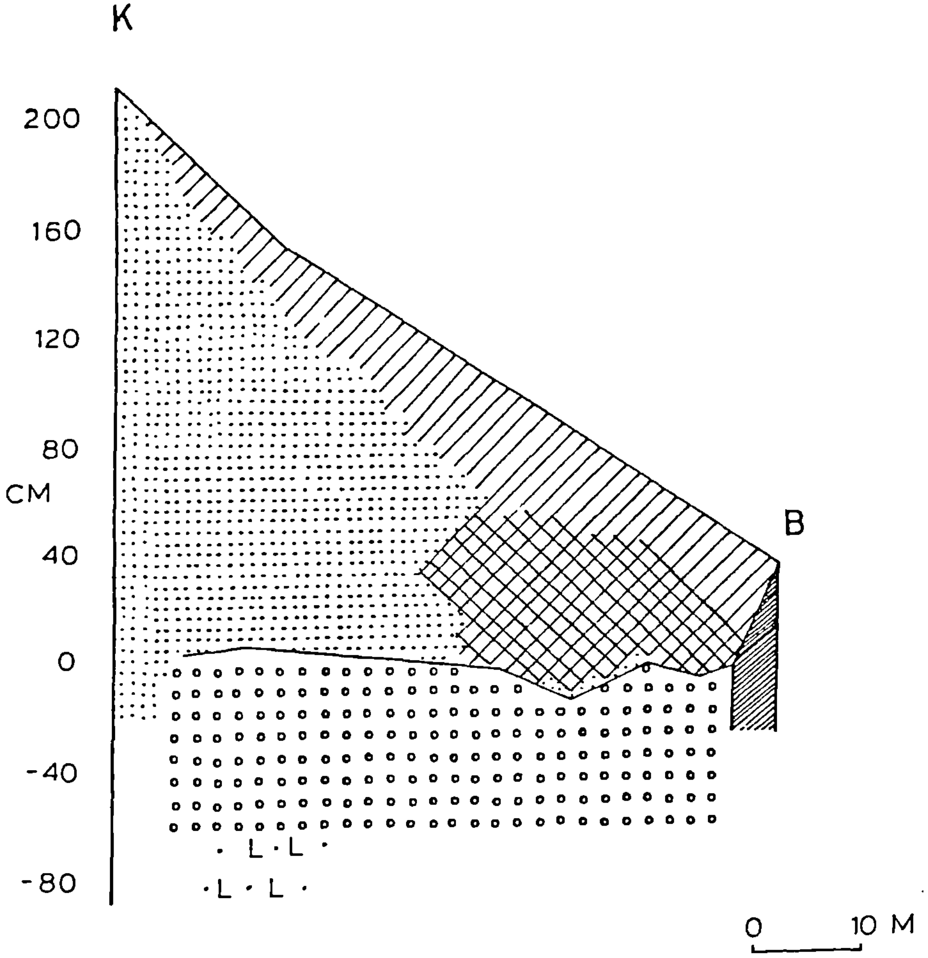


FIG. 2.4 CROSS-SECTIONAL TRANSECT THROUGH SEDIMENTARY DEPOSITS AT WILLOW GARTH.

periglacial conditions.

In the drainage ditch section the sandy hummocks appear to overlie well-sorted, stream-laid gravels, which in turn overlie gravelly sands containing angular flint and chalk fragments (Fig. 2.4 section B-K). These sands could perhaps be derived from soliflucted material. However, as the larger stones that might be expected in an in situ solifluction deposit are missing from this material, it is also possible that these deposits were the bed-load of a stream.

The gravelly sands appear overlie a thick (>1 m) deposit of a brown silty clay. This deposit is remarkably well sorted containing little material coarser than a fine sand. The general appearance of this material would suggest that it is derived from till, although in view of its well sorted nature, this would not appear to be an in situ till. It is possible that screw-augering is not the best way to sample this material and that the auger did not pick up the coarser material in the silty clay. However, as it appears to be so well sorted it is likely that this sediment may have been fluvially deposited in a very low energy or still water environment.

In another ditch exposure a series of lenses of sandy clays, ranging from white marly clays to yellow sandy clays lay beneath fen peats (Fig. 2.5 section A-B). These sandy clays were over 1 m deep. The bottom of these deposits could not be established but it is possible that they would overlie the brown silty clay found in the ditch section B-K. The brown silty clay indicated on section A-B (which contained no visible organic matter) was found to be rich in Carboniferous spores and only

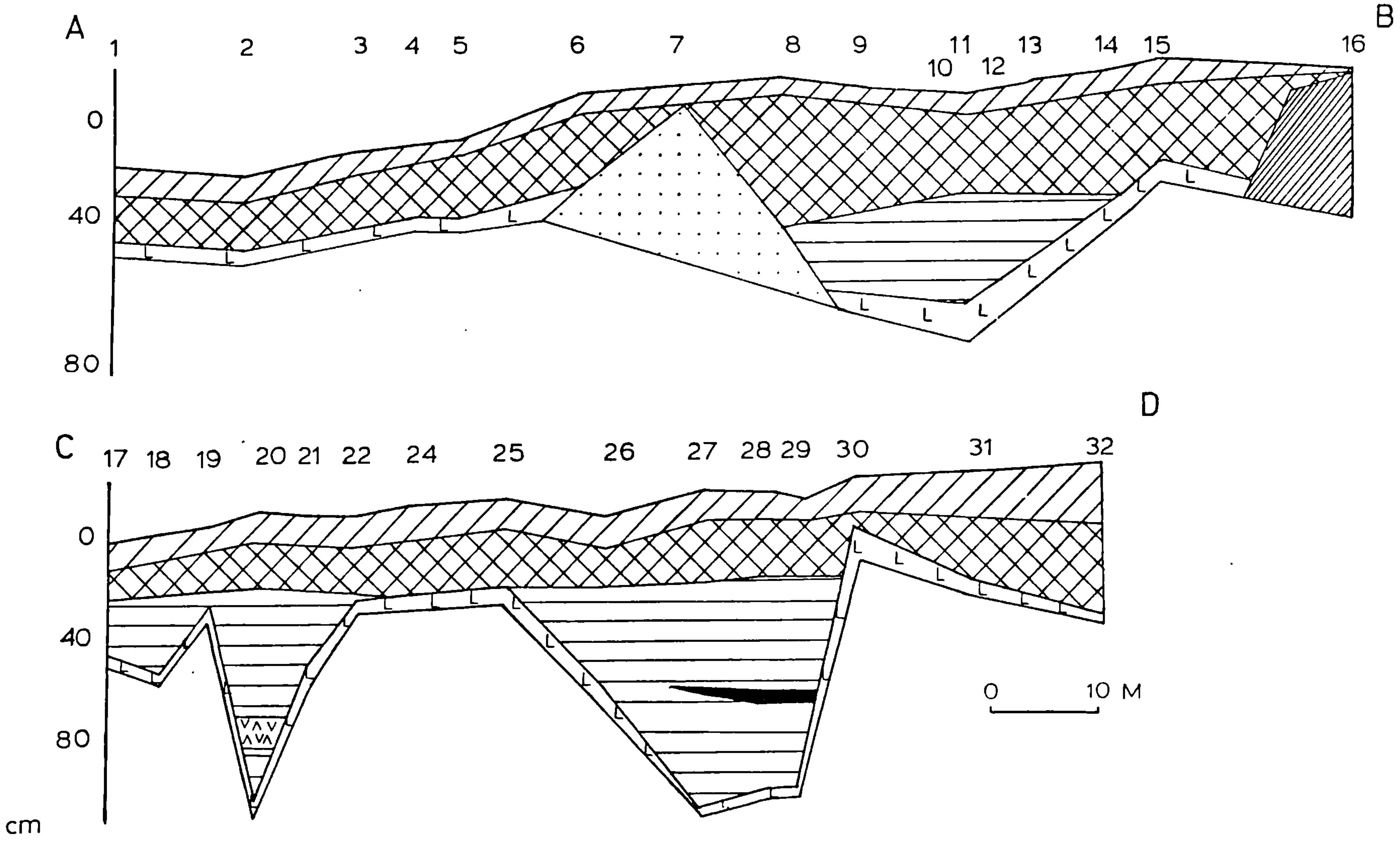


FIG. 2.5 : CROSS-SECTIONAL TRANSECTS THROUGH SEDIMENTARY DEPOSITS AT WILLOW GARTH.

contained pre-Flandrian Pinus pollen). It appeared similar to the loessic material deposited on the Wolds and Holderness at c. 18000 to 14000 B.P. (Penny et al., 1969) but had a higher clay fraction.

2.2.5 Willow Garth: The Depositional Environment

The history of sedimentation might be interpreted as follows. At c. 18000 B.P. there was an ice tongue lying near, or over, Willow Garth. Catt (1978) suggests that the Wolds had a bare rock surface at this time. In time the ice decayed leaving a thin till sheet on the hills to the south of Willow Garth. The subsequent ice retreat was accompanied by fluvial deposition, causing accumulation of the gravelly sands and gravels.

At the interface between the silty clays and the overlying stream-laid gravels there is a band of angular gravels in a white clay matrix. A high-energy depositional environment is indicated as some of the stones are up to 7.5 x 3 x 3 cm.

The stream laid pebbles and gravels (Fig. 2.4 section B-K) which overlie the clays suggest either the presence of a braided channel or, that for a period, the Gypsey race was running along the southern side of the valley. It would seem likely, in view of the absence of molluscs, that these channels date to the late-glacial period. The core analysed for its fossil content was collected about 30 m further towards the centre of the valley and yet it showed no trace of the coarse gravels associated with the braided channels. There is a sharp boundary between the start of the peat formation and the uppermost limit of the sandy clays, probably indicative of a change in the water-supply to this site.

It would appear likely from the ecological evidence that the flow into this hollow was reduced and mosses, aquatic and semi-aquatic plants began to choke the flow even further.

The simplest explanation of the lack of evidence for the braided channels extending across the fossil sampling site, i.e. that all the sandy clays shown in section A-B overlie the stream laid gravels, does not seem likely as the gravels lie c. 1 m higher than the known lowest level of these sandy clays.

One possible explanation would be that the sample site formed on an island in a braided stream and that the stream contracted before it could erode and overrun the island. Alternatively, the stream might have changed its course higher in the valley so that the drainage switched to the northern side of the valley without ever migrating across the valley floor. A further possibility is that the coarse gravels and the sandy clays are all part of one complex depositional sequence in which lenses of differently textured sediment were laid down according to the local rate of flow. Further work is being carried out by Dr S. Ellis to establish the direction of flow of the stream which deposited the coarse gravels.

The sandy clays analysed for their fossil content would appear to have been gradually eroded from the surrounding sand banks and deposited into hollows in the valley floor. Although laid down under a low-energy fluvial environment the sedimentary effect would have been not dissimilar to that of a small lake.

For the remainder of the post-glacial period the most complete evidence comes from the stratigraphy of the sample site

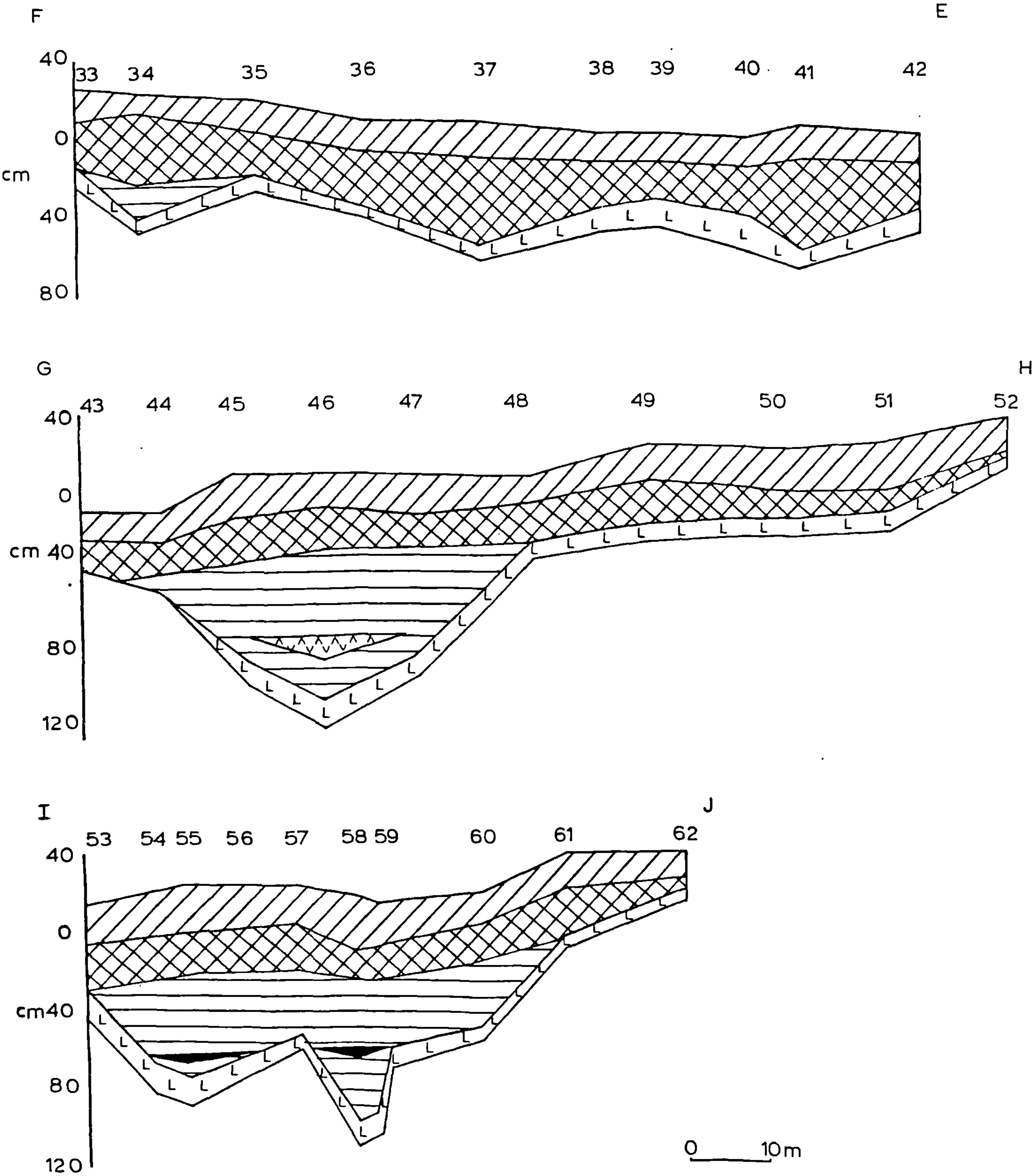


FIG. 2.6 CROSS-SECTIONAL TRANSECTS THROUGH SEDIMENTARY DEPOSITS AT WILLOW GARTH.

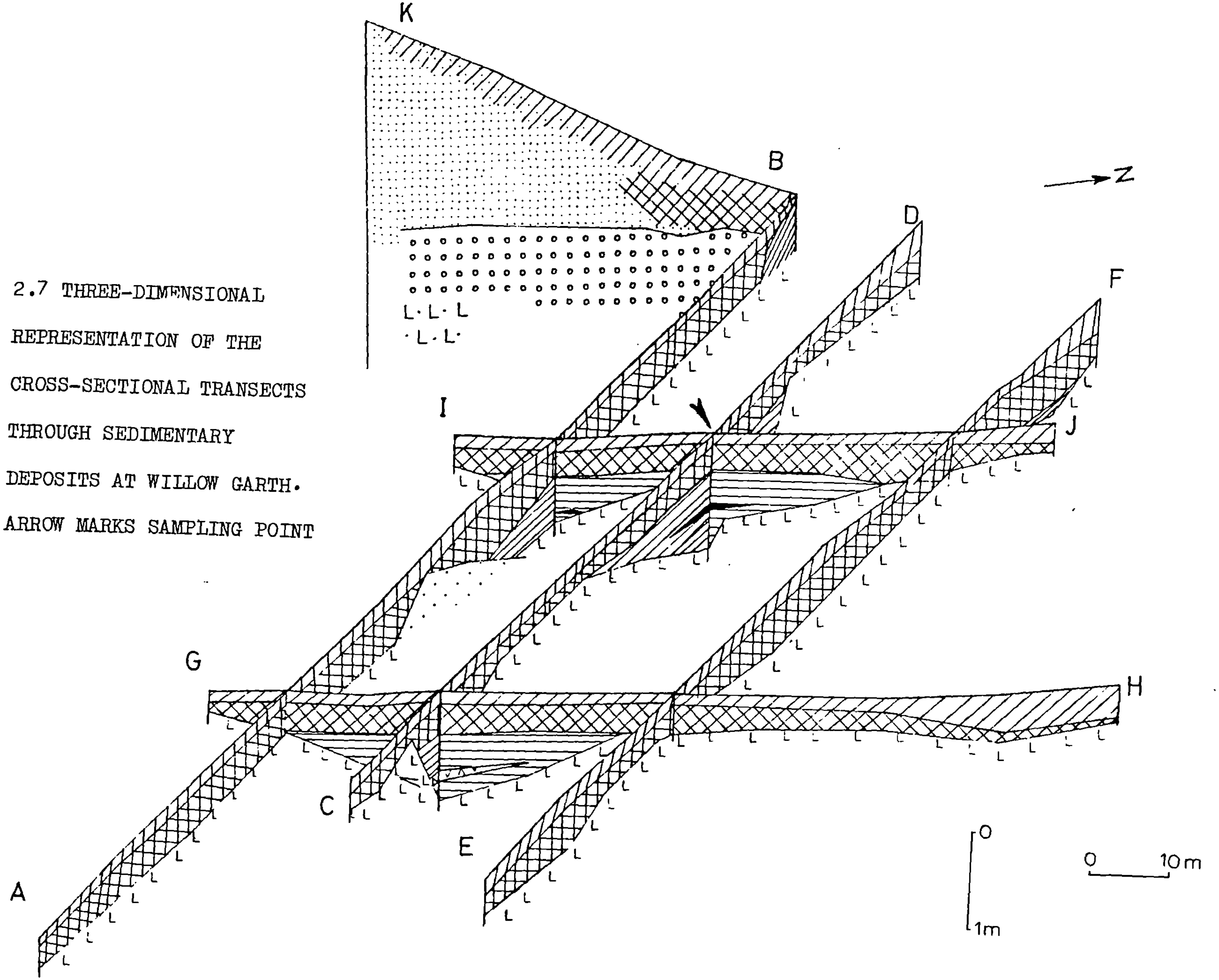


FIG. 2.7 THREE-DIMENSIONAL REPRESENTATION OF THE CROSS-SECTIONAL TRANSECTS THROUGH SEDIMENTARY DEPOSITS AT WILLOW GARTH. ARROW MARKS SAMPLING POINT

(Figs. 2.4 - 2.6). As can be seen from Fig. 2.7 the deepest organic deposit was located at the intersection of transects C-D and I-J. A number of further bore-holes were made to establish the greatest depth, the shape and the extent of this hollow. This depression was approximately 20 m x 20 m and had a maximum depth of organic material of 1.18 m, beneath this lay the pale brown sandy clay. The survey of the deposit indicated that this hollow was isolated from neighbouring, shallower, hollows and did not fit the pattern which might be expected for an abandoned meander channel. The origin of these hollows is unclear but they may be solution hollows or where there has been the collapse of a subterranean chamber in the chalk. Another possible origin for these features would be the melting of isolated ice blocks to form kettle holes.

It was not possible to penetrate the sandy clay layer beneath the peats using a peat-corer or a screw-auger, thus the sequence of deposits immediately above the chalk is not known. With the evidence available any suggestion as to the geomorphological origin of this site is speculative and best left until further data are collected.

Samples for the palaeoecological study were collected from the deepest sequence of organic deposits.

2.2.6 Willow Garth: Stratigraphy of Core for Palaeoecological Analysis

0 - 6 cm	Dark brown organic detritus containing rhizomes of *Iris pseudacorus* and leaves of *Salix* and *Populus*. No colour change on exposure to air. Dh^{1}3, Dl^{1}1, As+, Test. moll.+, humo 1, strf 0, elas 1, sicc 3, nig 3. Lim. gradual
7 - 30 cm	Khaki-brown organic-rich gyttja, no colour change on exposure to air. Ld^{4}4, Gg(min)+, Gg(maj)+, Dh+, As+,Test. moll.+, humo1, strf 1, elas 1, sicc 3, nig 3.
31 - 33 cm	Organic gyttjas identical to those above, but mixed with chalk fragments up to 50 mm x 20 mm x 8 mm. Ld^{4}2, Gg(maj)2, Dh+, As+,Test. moll.+, humo 1, strf 1, elas 1, sicc 3, nig 3.
33 - 48 cm	Khaki-brown organic-rich gyttja, no colour change on exposure to air. Ld^{4}3, Dh^{2}1, As+,Test. moll.+, humo1, strf 1, elas 1, sicc 3, nig 3. Lim. gradual
49 - 75 cm	Brown-black humified moss peat containing rhizome fragments and seeds, fine white sand present. Sediment turns brown on exposure to air. Tb^{3}3, Dh^{3}1, Ga+, humo 3, strf 1, elas 2, sicc 3, nig 3.

	Lim. sharp
76 - 82 cm	Mid-brown humified woody layer amidst moss peat, dark red-brown water-saturated timber, shrivelled and blackened on exposure to air. Tb^{3}1, Tl^{2}3, Dl+, Ga+, humo 3, strf 2, elas 2, sicc 3, nig 3. Lim. gradual
83 - 118 cm	Brown-black humified moss peat containing bark, timber and rhizome fragments and seeds, fine white sand present. Sediment turns brown on exposure to air. Tb^{3}3, Dh^{3}1, Ga+, humo 3, strf 1, elas 2, sicc 3, nig 3. Lim. sharp
118 - 136 cm	Pale coffee-brown coarse sands with clay fraction, contain timber and rhizome fragments. Gs2, As2, Dl+, Dh+, Test. moll.+, Tb+, humo 0, strf 2, elas 0, sicc 3, nig 2.

2.2.7 Willow Garth: The Pollen Catchment

In a model proposed by Jacobson and Bradshaw (1981) it was demonstrated how the pollen influx to a pond would be changed if a stream was to start to flow into the pool. The model suggested a peak of pollen influx at this time and a subsequent decline as the pool became overgrown, and the stream diverted elsewhere by peat growth.

Peck (1973) and Bonny (1976, 1978) have illustrated the importance of flowing water as an instrument of pollen transportation. In an elegant experiment Peck (1976) demonstrated that as much as 85% of the pollen influx to a pool with a feeder stream was waterborne. Pennington (1979) experimenting on Lake District catchments demonstrated that the pollen carried by an inflowing stream carried a greater regional component (80%) in an open landscape but that this was reduced to c. 45% in a densely forested environment. Pennington suggested that the relative importance of inwashed pollen would have varied during the post-glacial period. It is generally accepted however that an inflowing stream will greatly increase the effective surface area of a pool, in terms of its capacity to reflect the regional pollen component (Jacobson and Bradshaw, 1981).

At Willow Garth the size of the wetland area probably varied greatly during the late- and post-glacial periods. The individual pool which has yielded the deepest core, and what appears to be the most complete stratigraphic record, was probably only 40m x 60m (0.24 ha) during much of the post-glacial period. However the proximity of the Gypsey Race may have had an important influence on the addition of pollen to this sediment.

The flooding of the floor of the Great Wold Valley by the Gypsey Race can be traced through historical records back to early in the nineteenth century (e.g. Strickland, 1812).
Small quantities of fine sands are present throughout the moss peat deposit. These may have been derived from the bank overtopping of a clear chalk stream such as the Gypsey Race. It is not surprising to find a low silt content in these deposits as the sediment load of a chalk stream in an unploughed environment

is very low (C.Smith, 1980). A major input of water to the site probably came, as now, from springs. This appears to be sufficient to prevent the oxidation of the deposit. The past water regimes provided sufficient water to allow peat growth, however, it is almost impossible to dissociate the effects of increased spring flow at a site, from the capacity of a primarily spring-fed stream to flood. These are not, of course, mutually exclusive conditions.

One possible hypothesis would be, that to maintain the pools of water in which organic accumulation took place, spring flow and the chance of seasonal flooding were increased. The consequence of such flooding would be that the regional pollen, and to some extent the macrofossil, content of the sediment would be greatly increased. The Gypsey Race drains the largest watershed on the Yorkshire Wolds and so probably carries a large pollen component derived from a wide area of chalk. A seasonal flushing does not conform to the models of stream transport mentioned above and so the additional pollen influx through water-borne pollen cannot be estimated accurately. It would be fair to state, however, that the effect of such a regime would be to introduce a chalkland regional component far in excess of that which might be expected from a site of this size.

CHAPTER 3: FIELD AND LABORATORY METHODS

3.1 STRATIGRAPHIC SURVEY

Stratigraphic investigations were carried out using a screw auger to obtain an estimate of the depth of organic sediment at each site. Initial borings were made in the lowest lying areas, in spots which looked particularly promising, or where there was some evidence of organic rich soil at the surface. If any organic deposits were found to be more than 50 cm deep then a systematic pattern of coring was carried out using a D-section borer. Samples for laboratory analysis were described and bagged in the field.

3.2 SAMPLE COLLECTION

3.2.1 Fossil Pollen Samples

The preliminary core from Willow Garth had been collected using a D-section borer with a 25 mm chamber but this yielded insufficient quantities of sediment for a detailed palynological and radiocarbon sample analysis. For the major study a 72 mm diameter Livingstone Piston Sampler was used (Plate 1). In order to penetrate the layer of *Iris pseudacorus* roots the top 0.3 m was taken out as a monolith using a spade. The Livingstone corer was used to collect the sample from 0.3 m to 1.2 m. The depth of the organic deposit at this point was known to be 1.18 m and this was the depth to which the borer penetrated the ground before being stopped by the underlying sands. The sediment collected was only 0.88 m long including the surface monolith. There did not appear to be anything missing from the core, nor were there any

PLATE 1 EXTRUDING THE WILLOW GARTH POLLEN CORE FROM THE LIVINGSTONE PISTON SAMPLER (NOVEMBER 1982).

watery layers. It was concluded that the sediments had been compressed by this method of coring.

The samples were laid in plastic tubing and then wrapped in black polythene. Once labelled these were sealed and transported back to the cold store. They were stored in a darkened room at c. 4°C.

3.2.2 Modern Pollen Samples

The modern pollen sampling was carried out using pollen traps; some moss polsters were also collected to allow a comparison with the pollen trap data.

The cost of Tauber traps (Tauber, 1965) precluded their use in this project. It was necessary to utilise a trap suitable for collecting pollen in a variety of environments, which needed no maintenance, would not prove a temptation to vandals or the inquisitive (human or bovine) and could be produced inexpensively in large numbers. The design of the trap was taken, with certain modifications, from that advocated by Flenley (1973). The conical flask used by Flenley as a reservoir was replaced by an empty washing-up liquid bottle. Holes were pierced near the top of the bottle to prevent the reservoir from overfilling. Galvanised fencing wires were poked through the bottle (Fig. 3.1) to act as anchors to prevent the bottle being dislodged from the ground by wind, flooding or frost-heave. A further difference was in the diameter of the plastic funnel used. Flenley had suggested an 85 mm width funnel but in this study the plastic funnel was 72 mm internal diameter, matching the 72 mm internal diameter of the Livingstone Piston Sampler. The mesh used to cover the pollen

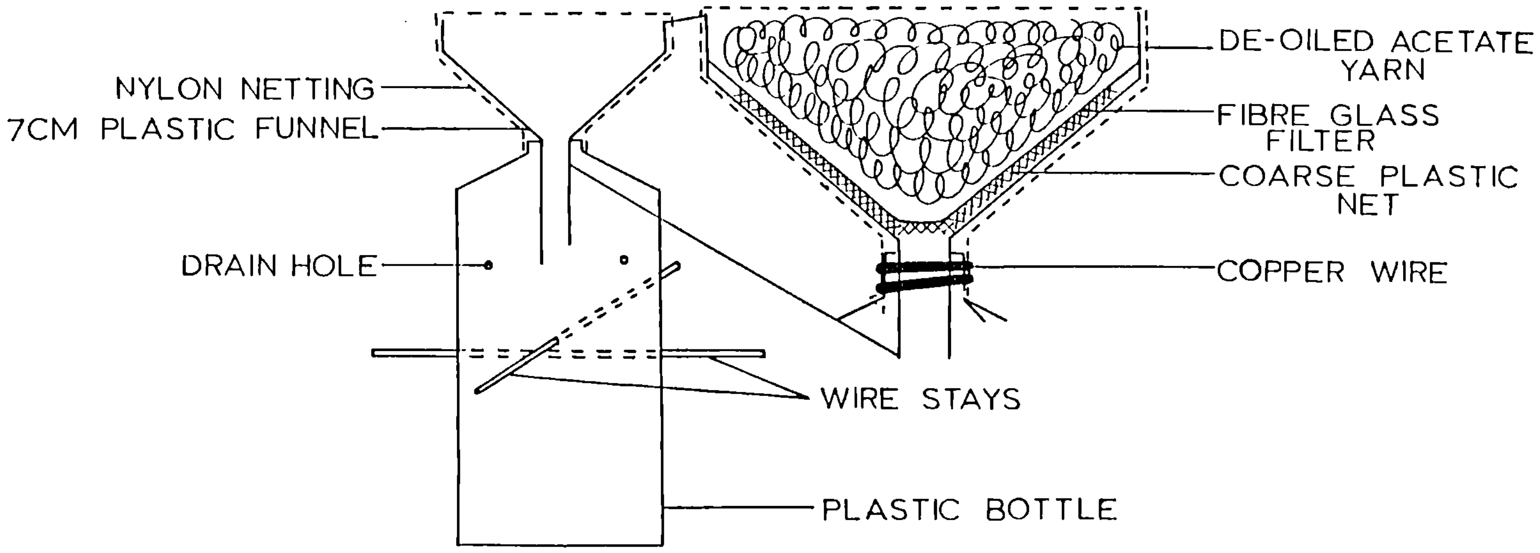


FIG. 3.1 A MODIFIED OLDFIELD POLLEN TRAP

PLATE 2 A MODIFIED OLDFIELD POLLEN TRAP IN THE FIELD.

(FLAMBOROUGH 5, MARCH 1983).

traps was a coarse gauze of the sort used to shade greenhouses. The reservoirs of the pollen traps were buried so that the rim of the funnel was 10 cm above ground level (Plate 2). The traps were left in the field for exactly one year.

3.2.3 Macrofossil Sample Collection

The 72 mm diameter core extracted from Willow Garth was not of sufficient volume to allow a detailed quantitative study of the macrofossil remains of this deposit. A second core was therefore necessary. This was taken from within 0.5 m of the first borehole in the following way. In June 1983 a pit was dug to the base of the peat. The water table was reached at c. 0.8 m down the hole, however the summer flow through the deposit was sufficiently slight for a face to be prepared and samples 40 mm deep x 200 mm x 200 mm to be removed and bagged sequentially to a depth of 1.36 m. The organic deposit was found to extend down to 1.18 m and the deposit below this was a stiff sandy clay.

The samples were bagged on site and then stored at 4°C in the cold store.

3.2.4. Modern 'Macrofossil' Assemblages

When the pollen traps were collected in the spring of 1984 the funnels were taken but the bottles were left in situ to mark the exact location of each trap. This provided the focus for subsequent vegetation and macro-remains studies. Samples to be used for macro-remains studies were collected between November the 10th and December the 5th, 1984. The late autumn was chosen because at this time there is the optimum seed bank in the soil

(Mittelbach and Gross, 1984) and there are the maximum number of molluscs at the surface (Paul, 1975).

Samples 10 mm deep x 300 mm x 300 mm were collected wherever possible. In some sensitive habitats, e.g. Fordon Chalk Bank, this was reduced, at the request of the warden, to 10 x 200 x 200 mm. The samples were bagged and labelled in the field. Bryophytes growing within 5 m of the site were also collected.

Those samples collected from aquatic habitats were gathered using a 2 m long, 10 cm diameter, perspex tube. The tube was pushed into the sediment to a depth 10 cm. By placing a bung in the top of the tube the tube could then be raised bringing the sediment, held in place by suction, with it. The bottom 8 cm of sediment were discarded. This process was repeated until _c._ 500 cc of deposit was obtained.

3.3 LABORATORY METHODS

3.3.1 Pollen

Slices of the sediment core to be analysed for their fossil pollen content were weighed, oven dried and then reweighed. From a known volume of sample, established by the diameter of the core, a known mass and therefore a known volume of the sample was removed to be used as the actual pollen sample. This portion was generally 0.3 - 1.5 g according to the sediment type. Preparation followed the procedures of Faegri and Iversen (1975). Spores of _Lycopodium clavatum_ were added to allow the calculation of pollen concentration and influx (Stockmarr, 1971).

The samples were put through an ultrasonic sieve (10 µm)

(Caratini, 1981; Tomlinson, 1984) as the final step before dehydration leading to mounting in silicone oil (200/12500 centistokes).

Pollen counting was carried out on a Nikon photomicroscope at x 300 with x 600 for detailed resolution and x 1000 for establishing surface structure. Phase-contrast microscopy was also used to determine pollen surface structure and for this the slides were transferred to a Zeiss photomicroscope which had the facility for phase-contrast at x 1000. Relocation of the grains was achieved using an 'England Finder' slide.

To extract the pollen from the modern pollen traps, the de-oiled acetate yarn and the glass-fibre filter paper were removed. Repeated washing with acetone dissolved the de-oiled acetate yarn and cleaned the surface of the filter paper. When the yarn was completely dissolved, distilled water was added. From this point the chemical preparation of the samples was identical to that used for the fossil pollen samples after the initial washing with potassium hydroxide. Exotic pollen was added to facilitate the calculation of pollen influx to the traps.

Moss polsters were first broken down using an 'Atomix' blender which minced the moss, so as to present a larger surface area for chemical attack once the acetolysis started. There was no point in drying or weighing these samples as it was not possible to carry out a comparable pollen concentration or influx calculation with that used for the fossil pollen. The chemical preparation was identical to the above procedure used for fossil samples.

3.3.2 Macrofossil Extraction

The technique adopted was disaggregation and separation through a bank of nested sieves as outlined by Kenward _et_ _al_. (1980).

The volume of sample used was estimated by the displacement of water in a large beaker. The sample size used was generally between 400 cc and 700 cc according to the sediment type. Once the volume of the sample was established the sample was poured into a bucket of hot water. The sample was allowed to soak for an hour, in which time the water was occasionally agitated by hand. The sediment was disaggregated by stirring with the hand and also by carefully teasing apart mats of peat or organic matter.

The sample was then poured into a nest of five sieves (2 mm, 1 mm, 0.5 mm, 0.3 mm and 0.2 mm mesh). A gentle stream of water was played onto the sieves to ensure that the finer particles were washed downwards. When all the sample had been treated in this way, if the uppermost sieve still contained material which could obviously stand further disaggregation this fraction was returned to the bucket and the soaking and agitation repeated.

Though this technique was outlined by Kenward _et_ _al_. (1980) for plant macrofossil extraction it was found to be effective for releasing molluscs and insect fragments.

Each sieve was then emptied into enamel trays and _c._ 5 cc subsamples were placed in a petri dish and viewed under a Watson dissecting microscope. The samples were lit by low power illumination from beneath and a strong oblique light, from a fibre-optic lamp. For most scanning and identification x 12.5 was found to be adequate, although for the surface pattern recognition of Juncus spp. fruits x 100 was used.

Specimens extracted from the samples were grouped on filter paper in petri dishes. The filter paper was moistened with a preservative mixture of 60 parts glycerol, 30 parts 80% alcohol and 4 parts 40% formalin. All plant remains were stored in this mixture. Insect remains were stored in absolute alcahol prior to mounting on card and molluscs were stored dry.

Identification of the various macrofossils was carried out using the keys of Smith (1978) and Watson (1969) for bryophytes, Janus (1982) and Kerney and Cameron (1979) for molluscs and Grosse-Brauckmann (1974) for rhizomes and stems. I am particularly indebted to the staff of the Environmental Archaeology Unit at York University for their help in teaching me to identify molluscs and plant propagules, and in identifying unknown material. In particular I should like to thank Dr A. Hall and Dr T. O'Connor. Dr H. Kenward provided all the entomological identifications and for this I am extremely grateful.

3.3.2 ORGANIC CARBON

As it was not appropriate to use the loss of carbon on ignition for calcareous soils (Ball, 1964) an estimate of the organic carbon content was obtained using a modified version of the potassium dichromate digestion technique proposed by Tinsley (1950).

i) 0.25 g of oven dry sediment were placed in a 500 ml flask and 10 ml of N $K_2 Cr_2 O_7$ were added.

ii) 20 ml of conc. $H_2 SO_4$ were added and the suspension agitated for 30 seconds. This was then left for 30 minutes.

iii) 190 ml of distilled water were added followed by 10 ml 88% $H_3 PO_4$. This was then left for 10 minutes.

iv) The suspension was titrated against 0.5 N $(NH_4)_2SO_4$. $FeSO_4$ (AFS) using 10 drops of 0.5% diphenylamine indicator (test titre).

v) A blank was prepared as above and titrated against 0.5 N AFS (blank titre).

vi) The normality of the AFS, which is rather unstable, was checked by titrating AFS against 10 ml of N $K_2 Cr_2 O_7$ with 50 ml of distilled water and 10 ml of $H_3 PO_4$; again 10 drops of diphenylamine indicator were used.

$$\text{Normality (N)} = 10 / \text{ml titre}$$

vii) The calculation for percentage organic carbon by weight was as follows:

$$\frac{0.3 \times (\text{blank titre} - \text{ml test titre}) \times N \times 1.33}{\text{mass of soil in g}}$$

3.3.3 pH

The pH of samples was estimated by taking a known mass of oven dry sediment to which distilled water was added, in the ratio 1 part sediment : 2.5 parts water, by weight. The mixture was stirred vigorously, allowed to stand for 10 minutes, stirred again and the pH of the suspension was then measured using a glass reference electrode pH meter.

3.4 RADIOCARBON DATES

The most obvious problem with the radiocarbon dating of sediments accreting in waters rich in calcium carbonate is the inclusion of 'old carbon' leading to erroneously old dates. Deevey et al., (1965) showed that if fresh water aquatic (submerged) plants utilise bicarbonate from ancient limestone as a source of photosynthetic carbon, they will appear markedly depleted in ^{14}C with respect to wood. As this is a problem resulting from the initial ^{14}C concentration of the environment it cannot be rectified by the application of $d^{13}C$ correction (Gupta and Polach, 1985). At Willow Garth the peat deposit was largely composed of mosses, the most abundant of which was Amblystegium riparium. This species is one which grows beside pools, although tolerant to inundation, it does not generally grow as a submerged species (A.Smith, 1978). Other species which made up the moss peat were: Drepanocladus spp., Calliergon spp. and Scorpidium scorpioides. These are all species which will grow in, or beside, a fen pool but are not obligate aquatic species. The relatively low numbers of submerged aquatic higher plant propagules compared with emergent or poolside species would suggest that the bulk of this sediment was composed of species which would have utilised atmospheric carbon rather than dissolved carbonates.

The separation of carbon into 'carbonate' and 'organic' carbon fractions isolated any carbonate not incorporated in the organic fraction. For the samples analysed at the Scottish Universities Research and Reactor Centre this was carried out by means of an acid digestion using 2M hydrochloric acid at 25°C.

The acid insoluble 'organic' fraction provided the substrate for most of the age measurements. Where acid hydrolysis resulted in the evolution of Co_2 this was collected and retained for comparable ^{14}C and/or $d^{13}C$ analysis.

The $d^{13}C$ could also be used to indicate whether the carbon was primarily derived from C3 plants, or CAM plants and C4 plants (Troughton et al., 1974). Troughton et al. observed that C4 and CAM plants generally yielded a higher $d^{13}C$ count (c. $-13^{o}/oo$), whereas C3 plants yielded a $d^{13}C$ value of (c. $-27^{o}/oo$). As the $d^{13}C$ for the 'organic' carbon fraction were all close to $-27^{o}/oo$ it is fair to assume that the majority of the carbon measured was derived from C3 plants.

A further problem with shallow deposits is caused by rootlet penetration. Whilst the obvious contaminants can be removed from a sample it is most unlikely that the sample can be picked clean of rootlets. At Willow Garth the trees can be seen to be shallow rooting (Plate 5) with plate-like root masses being limited by the saturated soils below 30 cm. Thus in the upper layers root penetration may cause dates to appear young but below 30 cm there was little evidence of rootlets and it is not thought that the dating has been seriously distorted from this cause.

In short, whilst there is always the possibility that 'old carbonate' has affected the C^{14} dates, no reason has been identified that makes these dates any more suspect than those from other chalkland sites. D. Harkness was consulted with regard to the suitability of this sediment for C^{14} dating and he was confident that accurate results could be obtained.

Two cm thick, approximately evenly spaced, samples were taken from the 7.2 cm diameter pollen core. The slices cut from the core for dating were inspected for contaminant rootlet pentration prior to being submitted for C^{14} dating.

3.5 THE POLLEN SUM

Amongst the first decisions to be taken when starting a pollen analysis is to determine the size of the pollen sum to be used. However, before this can be set it is necessary to decide which taxa are to be included within that sum and which, if any should be excluded. In part this will depend on the concentration of pollen and spores in the sample. Where concentrations are low all the pollen and spores might be counted and included in the pollen sum (e.g. Evans and Dimbleby, 1976). Where concentrations are higher some criteria for the selection of which taxa are to be excluded from the pollen sum may be excersised.

In this study the pollen sum is expressed as total dry land pollen, although the total pollen sum is also expressed for comparison. The definition of what constitutes dry land pollen is not always clear and here it is taken to mean non-obligate aquatic species. Some species which occur in fens produce pollen morphologically inseparable from species of the same genus to be found in dry land habitats, e.g. Filipendula ulmaria and Filipendula vulgaris. In these cases the taxon is included within the dry land count. Cyperaceae were excluded from the dry land pollen total on the basis that although an important component of grassland assemblages, the pollen yield from Cyperaceae was observed to be very low in the modern analogue study and that whole flowers of the semi-aquatic species might be directly incorporated into the sediments.

Some researchers choose to exclude Alnus from the pollen sum on the basis that the trees growing on the wetland will have been over-represented and can distort the data set (Janssen, 1959). Whilst this may have been necessary where high counts of Alnus were obtained, this was not felt to be the case at Willow Garth where Alnus seldom attained values greater than 10% of the total dry land pollen in the preliminary study.

The number of pollen grains recorded and the manner in which slides are counted is important for statistically valid results (Faegri and Iversen, 1975). The count must be sufficient to ensure that a random sample of the pollen grains present within the sample have been recorded. The size of this count will be a function of the species diversity of the sample. The dispersal of palynomorphs across a slide has been shown to be uneven (Brookes and Thomas, 1967) making it important to count entire, regularly spaced traverses. Birks and Birks (1980) stated that exact count reproducibility cannot be expected between slides. This applied to the taxa present as well as to the proportions of taxa.

3.5.1. Development of Method

If one particular taxon is extremely abundant it will have the effect of 'diluting' the other taxa in the sample. Thus if count sizes are fixed by a rigid count size an artefactual difference in diversity could be recorded from samples. To try to compensate for the presence of an highly abundant taxon species, diversity can be recorded against increasing count size and counting continued until the increase in species diversity is seen to be levelling off. The curves shown in Fig. 3.2 were obtained during this study and reflect varying degrees of 'dilution' by a common taxon; the flatter curves being those most affected. It may also be seen from this figure that the point at which the slide was changed often brought about a sudden upturn in the species diversity curve, as taxa not previously encountered were recorded on the new slide. Thus underlining the point that it is essential, if the full species diversity of a sample is to be recorded, to count more than one slide.

Dimbleby (1957) observed that in general all taxa which would eventually attain more than 1% of the pollen total had been recorded within the first 250 grains counted. It may be seen from Fig. 3.3 that the proportions of the dominant taxa, recorded in counts from fossil samples from Willow Garth, were relatively stable after c. 150 to 200 grains had been counted. This agrees well with data obtained by Barber (1976), who recorded that there was little variation in species proportion after the counting of the first 200 grains. This would suggest that 200 grains is the minimum count size to give reliable data. Birks and Birks (1980) recommended a count size of 300 to 500 grains according to the species diversity of the sample. Digerfeldt (1977) is amongst some of the continental workers who believe that counts in excess of 1000 grains are necessary. In an attempt to rationalise this argument and to offer international standards to be observed Berglund (1979) called for the standardisation of pollen counting

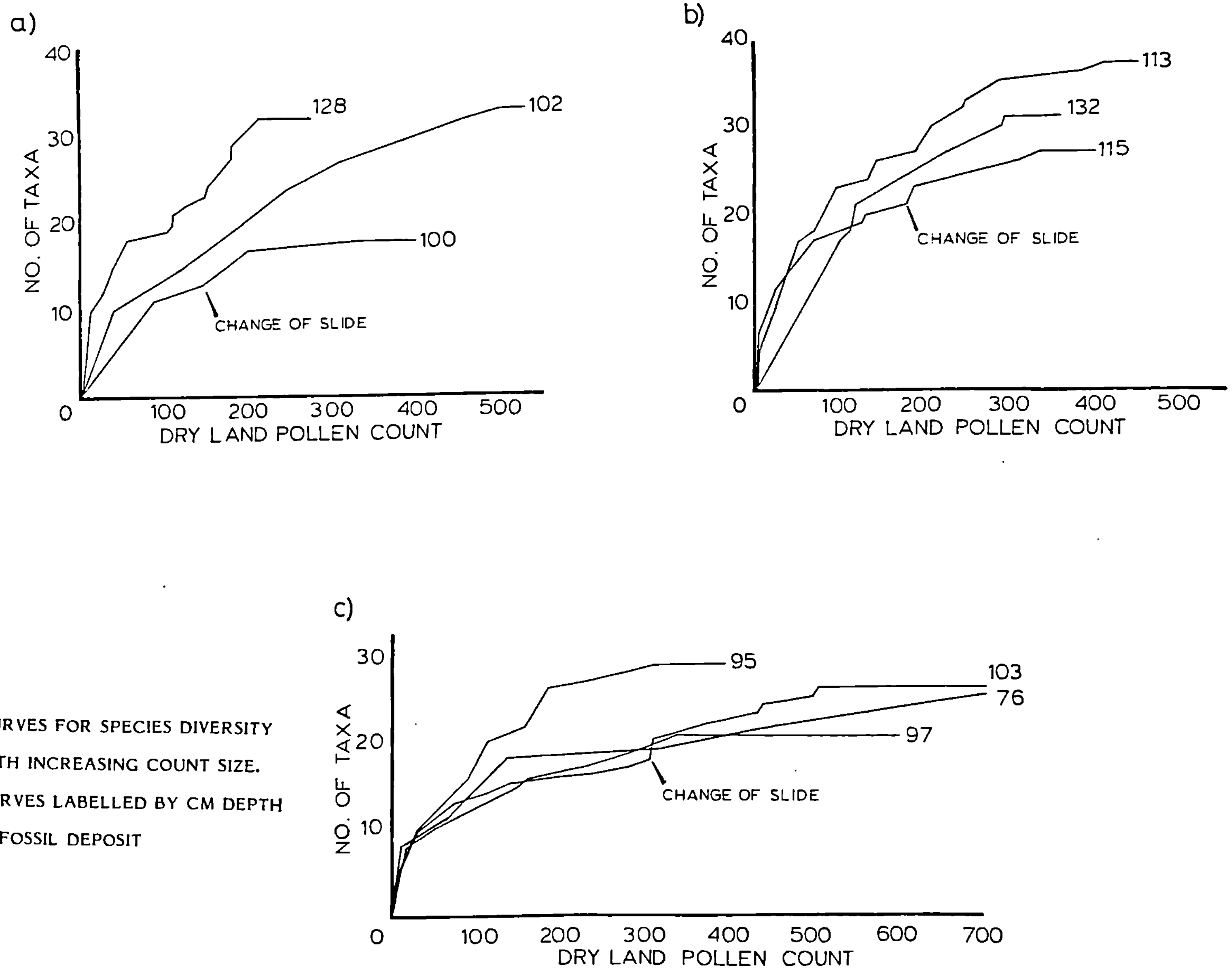


FIG. 3.2: CURVES FOR SPECIES DIVERSITY WITH INCREASING COUNT SIZE. CURVES LABELLED BY CM DEPTH IN FOSSIL DEPOSIT

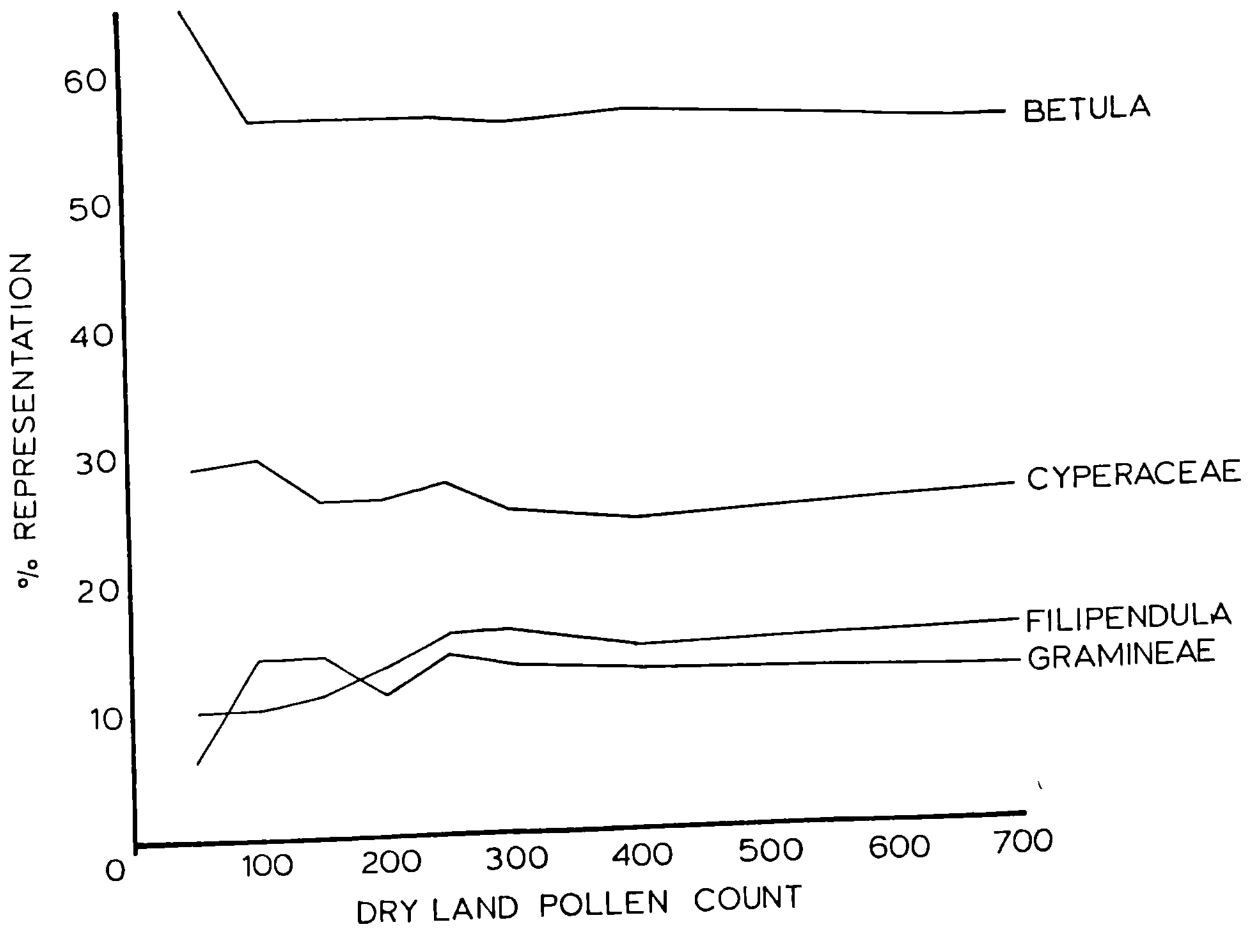


FIG. 3.3: % REPRESENTATION OF TAXA AGAINST INCREASING DRY LAND POLLEN COUNT SIZE.

DATA FROM THE FOSSIL POLLEN COUNTS FROM WILLOW GARTH.

procedures under the International Geological Correlation Programme (I.G.C.P.). This recommended the use of 300 to 500 dry land pollen as a 'normal' total.

For the present study this code was followed. 300 dry land pollen grains were counted wherever possible, but if the species diversity/pollen count curve had not approached a near equilibrium then the count was continued until the curve could be seen to have levelled off. In practice 400 to 500 grains of dry land pollen were counted for most samples, giving total pollen and spore counts as high as 1800. A minimum of four slides were counted and where pollen concentration was low as many as 12 slides would be used. Traverses were regularly spaced, with an average of c. 20 per slide. The use of 95% confidence limits (Mosimann, 1965) can be applied to key pollen taxa (Maher, 1972a) in order to try to reduce the effect of non-randomness in the pollen count. This helps to determine whether an observed fluctuation in a pollen curve is of statistical significance. The narrower the bars of the confidence limit the more convincing is a rise or fall in the pollen curve. As the dimensions of the error bars are negatively related to the pollen sum (Maher, 1972a) it is important to have a pollen sum large enough that some sensitivity to change is maintained in the diagram. From the diagram in Maher (1972a p. 91) it may be seen that a count in excess of 350 grains is necessary for this.

3.6 ABSOLUTE VALUES

3.6.1 Sedimentation Accumulation Rates

$$\text{The rate of accumulation} = \frac{\text{Deposition time}}{\text{Length of stratigraphic unit}} = \text{yrs cm}^{-1}$$

and; the years represented by 1 cm of sediment:

$$\frac{\text{Length of stratigraphic unit}}{\text{Deposition time}} = \text{cm y}^{-1}$$

3.6.2 Absolute Pollen Values

Pollen influx was calculated using the following equation (after Birks and Birks, 1980) :

$$P \times \text{sediment accumulation rate} = \text{pollen influx.}$$

where P =

$$\frac{\text{Fossil pollen counted} \times \text{Exotic pollen concentration}}{\text{Exotic pollen counted}}$$

Pollen concentration was estimated by the equation:

$$\frac{\text{Fossil pollen counted} \times \text{Exotic pollen added}}{\text{Exotic pollen counted} \times \text{mass of sample}}$$

3.7 CONVENTIONS

3.7.1 Stratigraphy

The stratigraphy of the samples from Willow Garth were described using the methods of Troels-Smith (1955). A five point scale was used to assess the abundance of the physical components in the sediment. Those properties described were as follows:

		abbreviation
Nigror	the degree of darkness	Nig.
Stratificatio	the degree of stratification	Strf
Elasticitas	the degree of elasticity	Elas
Siccitas	the degree of dryness	Sicc
Humositas	the degree of humicity	Humo

The deposit components observed were:

Turfa bryophytica	the basis of moss peat	Tb
Turfa lignosa	the basis of wood peat	Tl
Detritus lignosus	coarse woody detritus	Dl
Limus detritosus	organic lake mud	Ld
Argillea steatodes	clay (grains < 0.002 mm)	As
Grana arenosa	fine sand (grains 0.06 - 0.6 mm)	Ga
Grana saburralia	coarse sand (grains 0.6 - 2 mm)	Gs
Grana glareosa (min)	small gravel (2 - 6 mm)	Gg(min)
Grana glareosa (max)	medium gravel (> 6 mm)	Gg(max)
Testae molluscorum	mollusc shells	Test.moll.

All measurements are expressed in 'System Internationale' units although centimetres are used as they are a standard measure for pollen influx, e.g. grains per cm^2 per year. Whilst it is recognised that centimetres are not S.I. units they have been used here to facilitate comparison with other work.

3.7.2 Other abbreviations

gns cm^2 y^{-1} = grains per square centimetre per year (of pollen)

undiff. = undifferentiated

undt. = undetermined

B.P. = Before Present (see below)

Following the precedent of Birks and Birks (1980) late-glacial and post-glacial are given lower case initials and are hyphenated.

All radiocarbon dates are expressed as years Before Present, which is taken as being 1950 A.D., so as to avoid any possible confusion as to the reference date. All radiocarbon dates have been calculated using the Libby half-life value of 5570 ±30 years and have not been corrected to 'true' dates.

For the identification of pollen the nomenclature of (Benninghoff and Kapp, 1962) has been adopted.

sim. = strong similarity to indicated taxon, which may be a representative of several morphologically inseparable pollen taxa.

comp. = compares favourably with reference material but exact identification is uncertain.

The terminology adopted to describe the zones from which pollen has been derived are as follows:

local = pollen derived from within 20 m of the sampling site.

extra-local = pollen derived from between 20 m and several hundred metres of the sampling site.

regional = pollen derived from a source more than several hundred metres away.

(after Jacobson and Bradshaw, 1981)

In addition to these the term, 'adjacent' has been used in the following way:

adjacent = pollen which may have been derived from within 5 m of the sampling site.

3.8 POLLEN

Pollen zones (Godwin, 1940) have been shown to be time-transgressive (e.g. Turner, 1962) due to regional variation in rates of colonisation by plants and man. Pollen zones, despite these limitations, can still help in comparisons with other pollen diagrams. It is for this purpose that they are used here.

Betula nana, as opposed to Betula (undiff.), was defined according to the ratio of pore height to width of grain, given in Birks (1968).

3.8.1 Aggregate Groups

Type	Notes
Alisma	Contains Alisma and Baldellia.
Achillea	Round oval with dense interpattern between short spines, includes: Anthemis, Chrysanthemum and Matricaria.
Bellis	Similar to above but smaller and rounder, without interpattern, contains Eupatorium, Aster and Erigeron.

Bidens	Longer sharper spines than above, no interpattern, contains *Pulicaria*.
Cirsium	Includes *Carduus*.
Cyperaceae	No attempt was made to split this family as a large proportion were badly folded and the macrofossil record yielded a more detailed and reliable record for this difficult taxon.
Succisa	Includes *Scabiosa*
Epilobium	Includes *Chamaenerion*.
Apium	Small Umbelliferae pollen grain with long colpus and square pore, includes *Berula*.
Anthriscus	Larger Umbelliferae pollen than above, even width of exine around poles and lack of interpattern distinguishing it from *Heracleum*.
Vicia	Includes *Astragalus* and *Lathyrus*.

3.9 GRAMINEAE SIZE DATA

Gramineae form a major component of most pollen diagrams, indeed they are frequently the major component of post-forest-clearance phases. Despite attempts to identify Gramineae to a finer taxonomic level (Grohne, 1957; Faegri and Iversen, 1975; Andersen, 1978b) these techniques are extremely slow and difficult. Most palynologists only draw the distinction between *Cerealia* type pollen and Gramineae (undiff.), but even the definition of this distinction needs to be determined more accurately.

It is highly significant to determine the earliest occurrence of *Cerealia* type pollen at a site, but if the definition of what constitutes a cereal type is inaccurately specified then the misinterpretation of data may follow. Whereas some palynologists have drawn 37 µm as the minimum size for cereal pollen, there is strong evidence to suggest that non-cereal type Gramineae are capable of producing pollen attaining sizes of 40 - 50 µm (Beug, 1961). Grohne (1957), Beug (1961) and Andersen (1978b) have all attempted to define Cerealia pollen using phase contrast microscopy, minimum size and pore and annulus structure. None of these techniques has proved entirely satisfactory. The use of phase contrast microscopy by Grohne (1957) produced some very fine photographs of the exine sculpturing of a variety of cereal and non-cereal pollen types. Grohne suggested that the non-cereal pollen could be differentiated by the large and less regular pattern of raised areas, seen as dark patches under phase-contrast illumination. Though useful for highlighting different patterns on the surfaces of these pollen types the use of glycerol jelly in the mounting of the pollen used by Grohne prevents the comparison between these photographs and grains which have not been swollen artificially (Faegri and Iversen, 1975). The process of swelling would make structural elements much more distinct and separate than in unswollen or fossil grains (Faegri and Iversen, 1975).

The division advocated by Beug (1961) based on the sculpturing of the surface was criticised by Andersen and Bertelsen (1972). They had carried out scanning electron micrograph comparisons of the taxa described by previous authors and found all the classificatory systems lacking.

Rowley (1960) described the surface structure of Gramineae and his work was verified by that of Andersen (1978b), but neither technique was able to offer further information on the determination of cereal or non-cereal pollen for use with light-microscopy.

The Faegri and Iversen (1975) pollen key leads to 'cereal type' through a division between the grains greater than 40 µm and those less than 40 µm. If this division is followed there is then a key utilising some very subtle distinctions, which is difficult to use with any degree of confidence. To define cereal type pollen as that of greater than 40 µm is likely to exaggerate the presence of this taxon, as many of the 'wild' grasses will produce pollen of this size. For the purposes of this study Cerealia pollen were generally taken as being Gramineae pollen more than 44 µm long and with an annulus width greater than 10 µm (Andersen, 1978b). This is still not a foolproof system but it is unusual to find wild grasses with an annular width greater than 10 µm. A balance is therefore struck between the dangers of over-representation on the one hand, and lack of sensitivity on the other. Any definition of Cerealia is bound to be highly arbitrary until a better method of discriminating between the Gramineae family is found.

3.9.1 Gramineae: a Pool of Wasted Information

Once Cerealia has been split off from the rest of the Gramineae the remaining class, which is generally termed Gramineae (undiff.), or Poaceae, holds a mass of information which is lost to further interpretation. Jones and Newell (1948) demonstrated that most Gramineae taxa produced pollen of a characteristic size, and that the dimensions of the grains do not vary from one year to the next. It may therefore be expected that a given grassland community will produce a characteristic histogram of grass pollen sizes. If this spectrum changes within a pollen profile it may be assumed that the combination of grasses within that assemblage has been subject to change.

In order to plot any such changes the length of each Gramineae grain was recorded. A measurement of annulus width was also made of all grains greater than 40 µm long. This was carried out for both the modern analogue sites and the fossil pollen samples.

the measurement accuracy of the Nikon photomicroscope at x 600 is 1.3 µm. Clearly this does not permit the construction of 1 um size classes and so adjacent classes were paired to give the classes 16 - 17, 18 - 19, 20 - 21 ......76 - 77 µm.

The use of such a technique revealed significant changes in the size histogram for grass pollen analysed from Easter Island (Flenley and King, 1984). The patterns in the Easter Island data were clear to the observer and Flenley and King did not draw on any statistical techniques to consolidate their findings.

3.10 MACROFOSSILS

3.10.1 Propagules aggregate groups

Rubus fruticosus agg.	As defined by Clapham *et al.* (1962)
Cyperaceae biconvex	2 sided sedge nutlet including such genera as *Carex* .

Cyperaceae trigonous	3 sided sedge nutlet including such species as *C. heleonastes*, *C. riparia*, *C. flacca*.
Juncus articulatus agg.	very small seeds showing fine vertical striations and small cell structure. The intersection of cell walls raised to form a tiny spine.
Juncus conglomeratus agg.	surface pattern of large hexagonal cells, about 6 - 8 across the fruit.
Potamogeton polygonifolius agg.	small fruit *c.* 5 mm long.
Potamogeton praelongus agg.	larger fruit *c.* 10 mm long.

3.10.2 Molluscs aggregate groups

Cochlicopa lubrica	Most of this group were *C. lubrica* but some may have been *C. lubricella*.
Succinea putris	The testa of this species is only tentatively separable from *Oxyloma pfeifferi*. Some were definitely *S. putris* and so this name was adopted for the aggregate group.

3.10.3 Juvenile testa

The practice adopted by Preece and Robinson (1984) was to assume that the proportion of adults, reflects the proportion of juveniles. The total number of juveniles of similar species was divided by the proportion of the adults present in the samples.

This was the practice adopted in this study.

3.10.4 Incomplete testa

The counts of molluscs are based on the number of apices, or in the case of bivalves, hinge fragments. This avoids the over-representation of broken testa.

3.10.5 Bivalves

The count of individual valves was divided by two and in the event of a non-integer the product was rounded up.

3.11 NOMENCLATURE

The nomenclature follows that of the authorities listed below:

Higher plants	(Clapham _et_ _al_., 1983)
Bryophytes	(A. Smith, 1978)
Molluscs	(Kerney and Cameron, 1979 (terrestrial) and Janus, 1982 (aquatic))
Insects	(Kloet and Hincks, 1945)

CHAPTER 4: STATISTICAL METHODS

4.1 VEGETATION SAMPLING

4.1.1 Experimental Design

It was not the object of this survey to replicate earlier excellent surveys of chalkland habitats by such workers as Tansley (1939), Shimwell (1971ab) and Wheeler (1980a,b,c), but to obtain information relevant to the interpretion of modern pollen and propagule production. With any data gathering it is important to decide from the outset why the survey is being undertaken and what is required from the analysis in terms of the precision of data collection and recording, and the scale of the study. The level of identification in the field needed to be at least as accurate as that attainable through pollen or seed analysis. However to identify some taxa to species in the field, when the pollen of these taxa cannot be determined beyond aggregate groups, would seem to be going into unnecessary detail. The criterion for the level of plant identification was the level to which pollen or propagules could be identified with certainty.

The choice of a method for recording the vegetation needed to take into account arboreal taxa and communities of herb flora as diverse as tall fen associations to short cropped grassland swards. It was decided to make no attempt to combine the arboreal and ground flora surveys but to treat the two as separate problems requiring separate solutions.

4.1.2 The Herb Flora

Having decided on the level of determination required from the survey, it was then necessary to decide on the survey technique. The data were required to provide an estimate of the proportion of each taxon in each location. Mueller-Dombois and Ellenberg (1974) recommended canopy cover as one of the better indices in estimating the importance value of plant species. One of the strengths of canopy cover as an estimate is that it allows the comparison of widely different growth forms (Mueller-Dombois and Ellenberg, 1974). Floyd and Anderson (1982) list three basic techniques of canopy cover estimation: the use of quadrats, the use of line intercept methods (Cranfield, 1941) or the use of point intercept methods (Levy and Madden, 1933).

During the preliminary survey quadrats had been used to carry out a vegetation survey on short forb rich chalk grassland at Wharram Percy and in the tall fen communities of Willow Garth. These surveys were considered inadequate on the grounds that the technique applied was not sufficiently versatile to give comparable results in such widely differing vegetation types. For this reason it was decided to utilise either the point intercept or line intercept methods. Whitman and Siggeirsson (1954) compared these two techniques and found them to give equally representative results. Point intercepts gave slightly higher values for vegetation cover, although as Winkworth (1955) stated this does not necessarily indicate that the technique is more accurate. For the purposes of the present study it is important to have as complete a representation of the local species diversity as possible and again, so long as all the vegetative contacts were counted there was no difference between the two techniques. If however, only the base of each plant was scored then the line intercept method showed a significantly better representation than the point intercept method (Whitman and Siggeirsson, 1954).

The dispersal of pollen and seeds is such that the plants close to the point of collection are likely to have a better chance of representation than those further away. The survey technique could reproduce such a bias by having more samples closer to the centre of the quadrat than further away. Whilst this could be done using restricted random numbers and a point frame, it could also be achieved through radiating lines along which the line intercept method is carried out. As this latter technique had been proved to yield consistent data in a wide variety of habitats and because the line-intercept method was proven to give a more reliable species total, especially when plants are not fully in flower (sensu Whitman and Siggeirsson, 1954), it was decided to adopt this method.

As the vegetation surveys were to be carried out on only one occasion at each site it would be unrealistic to hope that all the plants would be at an equal stage of development; for this reason it was not practical to record only the flower heads. A survey of the basal portions of the plants was shown to leave a higher proportion of species unrecorded than the recording of all parts of the plant body (Whitman and Siggersson, 1954). This would inevitably lead to some errors in the recording, particularly of tussock species (Greig-Smith, 1964) or of those species likely to flower early and then die back, or those which do not fully develop until late in the season. These problems can to some extent be overcome by timing the survey carefully, so that the woodlands, where the herb flora will die back early in the summer, are surveyed first and the open ground habitats a little later. The tussock species present a problem to accurate recording and the best that can be hoped for is a close approximation to the number of contacts along the line. The accuracy of this can be improved if the line is subdivided. In this survey the number of contacts along each 0.5 m length of the line were recorded, but when there was tussock vegetation this recording length was reduced to 0.1 m.

The results therefore must be seen as a good approximation rather than a true absolute technique. The statistics applied to these results should therefore be robust, capable of handling ecological data and capable of handling a data set containing many (>50%) zero values. There should also be a mechanism within the analysis which deals with the data set in a semi-quantitative manner, so that orders of magnitude are recognised within the scale of the data set. This would overcome the problem of establishing exactly how many blades of grass there were in a tussock and yet provide a far more accurate estimate than 'frequent' or 'abundant'. The number of contacts may be an estimate but again it is more accurate than a simple Domin scale of 1 to 10, and is therefore preferable if at any future stage it is decided to attempt a comparison of the number of vegetation contacts and the absolute representation of pollen.

The length of the transects was chosen to be comparable with the work of Ryvarden (1971a,b) and GreatRex (1983) who had both measured the seed representation of plants growing within a 5 m radius, and also the work of Tauber (1965) and Handel (1976) who had suggested that the majority of herb pollen will be deposited within 5 m of its production.

The location of the pollen trap formed the focus of 8 radiating transect lines aligned to the major points of the compass; each was 5 m long, subdivided into ten 0.5 m lengths. The transect was considered as a vertical plane, and the number of contacts of stem, leaf, pinnule or flower along that line were recorded for each 0.5 m unit. Any species which were present within 5 m of the sample site but were not recorded by the line transects were noted separately, with annotations such as frequency and distance from trap.

The point at which the pollen trap had been sited could be relocated exactly because when the pollen traps were collected at the end of March 1984 the bottles had been left in situ to mark the centre of the vegetation quadrats to be recorded during the summer. Thirty four pollen traps were recovered but vegetation analyses were carried out at only thirty three sites as the vegetation of one, Kiplingcotes 3, was burnt between the collection of the pollen trap in March and the vegetation survey in June.

4.1.3 The Arboreal Flora

The object of this survey was to obtain data on the species representation within the canopy for comparison with pollen and seed data from the same site.

For this it was necessary to utilise an index of forest cover which gave an impression of the relative importance of the taxon. The standard measurement of the girth of a tree at 1.3 m above ground, as utilised by Bradshaw (1981a), gives an estimate of the standing wood in a forest. However, it does not provide a direct measurement of the flower producing portion of the tree, the canopy. As it is the flowering capacity which is most likely to influence the production of pollen and propagules it is desireable that some measurement of the canopy area is made. To estimate the area of the canopy from the ground calls for time-consuming measurements unless a flexible model of tree shape can be proposed. From subjective observations of tree shape it appeared that most trees form an essentially domed canopy. This may be flattened or acute in shape, but of simple geometric shapes a dome would appear to represent the closest approximation for most species. The base of the dome was not required as it appears that the foliage and flowers borne in this portion of the canopy are a small proportion in relation to those borne on the exterior of the dome. As flower production generally takes place on the edge of the canopy and is not uniformly distributed throughout the volume of the canopy, canopy surface area would be a better estimate of the flowering capacity than volume.

The surface area of a dome can be established from the calculation of the surface of revolution of half an ellipsoid (C. Smith, 1966) as given below:

If the canopy width b is greater than the canopy height a:

$$A = 2\pi bK\left[\sinh^{-1}\frac{a}{K} + \frac{a\sqrt{(K^2 + a^2)}}{K^2}\right]$$

Where A = the surface area of the dome, and where:

$$\sqrt{\frac{1}{a^{-4}(b^2 - a^2)}} = K.$$

If the canopy width b is less than the canopy height a:

$$A = 2\pi bH\left[\sin^{-1}\frac{a}{H} + \frac{a\sqrt{(H^2 - a^2)}}{H^2}\right]$$

Where A = the surface area of the dome, and where:

$$\sqrt{\frac{1}{a^{-4}(a^2 - b^2)}} = H$$

This formula requires the following measurements:

a) the height of the tree

b) the height of the lowest branches of the main canopy

c) the mean diameter of the canopy

The radius of the survey from the sample point must also be defined, this is best related to the distance which the majority of the pollen will have travelled. Pollen dispersal within woodlands has been the subject of considerable research (Tauber, 1965; Andersen 1970; Raynor et al. 1974, 1975). Andersen suggested that in woodlands the majority of pollen collected at a point had originated within the surrounding 20 to 30 m. Bradshaw (1981a) studied the pollen representation in British woodlands, comparing pollen yield with the flora of the surrounding 20 m. The same distance was adopted in this study to render the results comparable with those of Andersen (1973) and Bradshaw (1981a). As seeds are generally distributed over shorter distances than pollen (Birks and Birks, 1980) this area would presumably contain the majority of trees from which the propagules will have been derived.

In order to facilitate the mapping of the canopies of individuals of each species within the wood the following were recorded:

a) the species name
b) the distance to the base of the tree from the sampling point
c) the compass bearing to the base of the tree from the sampling point
d) the distance to the nearest edge of the canopy from the sampling point

This last measurement was made in order to ascertain whether the canopy was excentrically located above the trunk.

So that the correlation between the canopy measurement and the pollen production could be checked against the measurements used by Bradshaw (1981a) the girth of each tree was measured at 1.3 m above the ground. In this survey a tree was defined as any lignaceous plant with a girth in excess of 20 cm at 1.3 m above the ground. Where stools had been coppiced these were included in the survey even if the individual stems had a girth less than 20 cm. The selection of 20 cm as the minimum girth size to be recorded was to provide comparability with the work of Bradshaw.

4.2 CANOPY AREA AS AN INDICATOR OF POLLEN PRODUCTION

Using the data gained from the woodland surveys, and from the pollen traps, the woodland composition could be compared with the pollen production. In order to test the hypothesis that canopy area was a more accurate index of pollen production than basal area both were calculated and compared.

The absolute canopy area for each species could then be plotted against its absolute pollen representation for all the plots in which either the tree and/or the pollen was recorded. In almost all cases this resulted in a distribution of points which were clustered around the origin of the graph, with only a few outlying points. Bradshaw (1981a) obtained similar results. Such a highly skewed distribution is unsuitable for regression analysis (Hammond and McCullagh, 1975) but as both axes showed a strong positive skew it was possible to normalise the data set by taking the square-root of both the absolute pollen yield and the absolute canopy, or basal area. In doing this the data set is not fundamentally changed or distorted but tight clusters of points, particularly those grouped at the origin, will be spread along both axes. The data set will then have a sufficiently normal distribution to allow regression analysis (Hammond and McCullagh, 1975).

The results of the initial analysis showed that the canopy area was a more efficient technique for establishing the proportion of pollen representation, as indicated by the size of the residual, for species which had been coppiced. This was largely the result of the difficulty of measuring the basal area of a coppiced stool. Flower production from such a stool is known to be reduced (Bradshaw, 1981a) and the girth frequently over-estimated so that the pollen representation appears strongly under-represented. Canopy areas proved to be an improved method of representation in these cases, but were no better, and sometimes worse than basal area, when dealing with other growth forms (Table 4.1). Thus the initial hypothesis must be rejected at this stage.

One aspect of canopy area which had not been taken into account in the original calculation was the density of the canopy. Trees of equal canopy area, as determined by canopy height and canopy width, could have quite different crowns. One could be lax and open, bearing relatively few flowers, whilst the other could be a dense, closed canopy carrying many flowers. In order to allow for the variation in density between crowns it was necessary to apply a weighting to the canopy area. This weighting was taken to be the circumference of the trunk at 1.3 m above ground.

Nutrients, created by photosynthesis, are stored for the winter in the medullary rays (Salisbury and Ross, 1978), and the most active portion of these rays lies close to the phloem (Kramer and Kozlowski, 1979). Early in the year these nutrients are transported to the crown of the tree where they provide the energy for leaf and flower initiation (Kramer and Kozlowski, 1979). As these nutrients are stored in the outer portion of the trunk in most trees, the circumference of the trunk offers a better index to the nutrient storage capacity than the basal area, which would contain a high proportion of dead and inactive medullary regions. When the canopy area was multiplied by the circumference the product was termed the weighted canopy area. After this had been calculated for each species, at each site the normalised data was plotted against the normalised absolute pollen (Fig. 4.1). This produced a scatter of points closer to the best fit regression line than basal area or canopy area. This is shown in Table 4.1 where the square of the residual for each species, obtained from the regression analysis is presented.

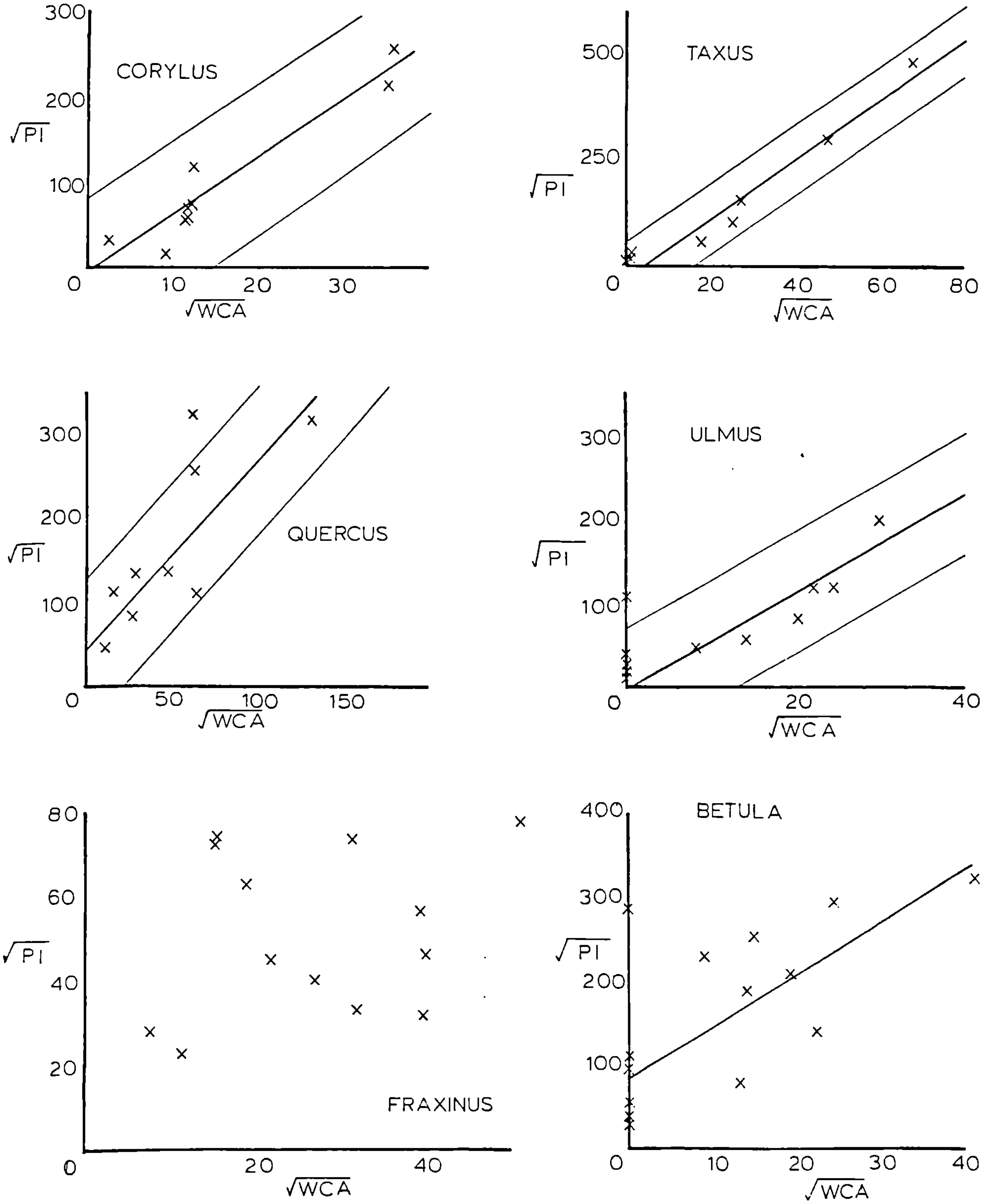
TAXON	BASAL AREA	CANOPY AREA	WGTD CANOPY AREA
Acer	2575	2025 *	2236
Betula	27782 *	28625	27969
Corylus	7885	13338	5375 *
Fraxinus	941 *	1580	1685
Quercus	17309	11145	9694 *
Taxus	13585	11194	9525 *
Tilia	3244	1750	147 *
Ulmus	7317	5179 *	5230

* = lowest residual variance

TABLE 4.1. Residual variance from regression of modern arboreal pollen.

It will be noted that the weighted canopy area gave not only the highest number of best correlations but it moderated the degree of variability so that it gave the second best estimate in three out of the four remaining cases. Only in the case of _Fraxinus_, for which none of the methods gave a significant result, did the weighted canopy area yield the poorest correlation.

The hypothesis may now be amended to: The weighted canopy



WCA = WEIGHTED CANOPY AREA PI = POLLEN INFLUX

FIG. 4.1: BEST-FIT REGRESSION LINES AND 90% CONFIDENCE LIMITS APPLIED TO THE POLLEN REPRESENTATION OF SELECTED ARBOREAL TAXA FROM MODERN POLLEN SAMPLES.

area provides an improved index for correlation to pollen production over that provided by canopy area or basal area alone.

4.3 R-REL VALUES

R-rel (Andersen 1970, 1973) was a refinement of the R values (Davis 1963) proposed to quantify the relationship between the abundance of an arboreal taxon and its pollen production. From this relationship a weighting could be derived for each taxon and this then utilised in the interpretation of species abundance in fossil pollen spectra.

Andersen (1973) suggested that the majority of pollen deposition within woodlands took place within 20 m of the pollen source. Therefore a vegetation survey of 20 m radius should provide sufficient data to correlate with the pollen input to the central point. An indication of the amount of pollen derived from the extra-local woodland can be obtained from the intercept value of the regression analysis (Fig. 4.1 and Table 4.2). Betula had the highest intercept value of the trees recorded in the vegetation plots. The value for Pinus was not available as no Pinus was recorded from any of the plots and yet the pollen was recorded from almost every pollen trap.

TAXON	INTERCEPT	SLOPE	CORR. COEFF.	N	SIGN.
Acer	-0.21 ±0.22	1.18 ±0.38	0.82	14	0.01
Betula	1.23 ±0.27	3.17 ±0.67	0.82	14	0.01
Corylus	0.42 ±0.20	2.78 ±0.53	0.83	12	0.01
Fraxinus	0.61 ±0.19	0.25 ±0.22	0.33	13	
Quercus	1.00 ±0.30	1.00 ±0.22	0.86	9	0.01
Taxus	-0.57 ±0.34	3.63 ±0.36	0.97	7	0.01
Ulmus	0.07 ±0.54	2.91 ±0.96	0.83	6	0.05

Table 4.2. The results of the regression analysis of woodland taxa. Slope and intercept coefficients are relative to those for Quercus (after Bradshaw, 1981a).

The intercept value and its confidence limits reflect the extra-local pollen component, whereas the slope of the regression line reflects the pollen/weighted canopy area relationship. It can be seen from Table 4.2 that Taxus and Acer both had negative intercepts. This implies that there needs to be a substantial canopy area of both species before any pollen is deposited. This could merely be due to the size of the samples used, but an explanation can be offered for both species.

Acer would seem to be an under-producer in most woodlands. Bradshaw and Webb (1985) suggested that this might be due to its adaptation to entomophily. A different cause might be cited for Taxus and that is that as an understorey tree it is a poor pollen producer. Bradshaw recorded this from the Mens and the Cut Wood where Taxus was poorly represented in the pollen totals. However, in samples from the New Forest where Taxus was a component of the upper canopy it flowered abundantly and was well represented in the pollen spectra (Bradshaw, 1981a). In this study high Taxus counts were only recorded from the Kingswood where Taxus was growing as a canopy tree.

The only non-significant correlation coefficient obtained from the regression analyses was for Fraxinus (Fig. 4.1). Where there were plots with a few large Fraxinus present, the pollen production of this taxon was relatively high. There were however some sites where many immature Fraxinus were growing. The combined total canopy area for these trees was large, because of the density of the stand, but they were producing very little pollen. The non-significant result for this taxon and the lack of data points for Tilia meant that the R-rel values for these species were taken from the results of Bradshaw (1981a) and Andersen (1970) respectively.

The pollen traps had been set in a variety of ancient woodland habitats. These woods were treated as representing one broad deciduous forest type, taking into account as wide a mixture of species as possible. The R-rel value obtained from this data set would be a generalised correction to apply to a broad spectrum of forest types likely to be found on the Yorkshire Wolds. Given that the climatic and edaphic factors may have changed very considerably during the post-glacial period the utility of highly specific R-rel values established for each wood as used by Bradshaw (1981a) is perhaps open to question; a broad based correction may be of more use.

TAXON	R-REL; THIS STUDY	R-REL; BRADSHAW
Betula	7.6	1.5; 16.0; 17.3
Corylus	3.0	N/A
Ulmus	2.1	N/A
Taxus	1.8	1.7
Quercus	1.0	1.0
Acer	0.5	N/A
Fraxinus		1.2
Tilia		0.3

TABLE 4.3. R-rel values for arboreal taxa ranked from highest to lowest.

R-rel values used in this study were obtained by summing the absolute pollen representation for a given taxon, summing the weighted crown area values for that taxon and then dividing the former by the latter, so as to obtain an R value which was then divided by the R value for Quercus to obtain an R-rel value.

The degree of over-representation of Betula was more marked in the woods studied by Bradshaw. Although he obtained a range of values from 1.5 to 17.3 according to the woodland type, he utilised an overall R-rel value of 16.0 (Bradshaw, 1981a). One reason for Betula not being so over-represented in the present survey may have been that the calcareous soils of the woodlands sampled in the present study might not suit Betula as well as the heavier, more acidic soils of the southern woodlands.

In general there would seem to be broad agreement on the slopes of the regression lines and the points of intercept of the two studies.

4.4 ORDINATION

Since the introduction of Polar Ordination by Bray and Curtis (1957) there have been many attempts to apply refined versions of this technique to ecological data (e.g. Loucks, 1962; Cottam et al., 1973). Principal Components Analysis (P.C.A.) was introduced by Orlocci (1966) and was widely used during the 1970s. This technique had the advantage of an objective definition of its axes, but it was found to produce uninterpretable results if used on curvilinear or non-monotonic data sets (Beals, 1973). The common fault was the production of an arch or horseshoe shaped curve which implied a relationship on the second axis which was entirely a product of the statistical analysis (Noy-Meir and Austin, 1970).

One advancenment on P.C.A. was RECIPROCAL AVERAGING (Hill, 1973), or correspondance analysis, (Benzecri, 1969). This was a technique based on obtaining weighted averages from repeated iterations from which a calibration for each species could be calculated. The 'arch effect' was much reduced but still apparent (Kendall 1971, Gauch et al., 1977). A further, and it is claimed, to date the most suitable ordination technique for ecological data, has been presented by Hill and Gauch (1980). This technique, Detrended Correspondance Analysis, DECORANA, differs from reciprocal averaging in two main respects. Firstly, through the rescaling of axes to obtain a more even spread of points along each axis and secondly by ensuring that the second, and subsequent axes, are derived so that there are no systematic relationships between the higher axes and the first. In this way it is hoped that the ecological distances represented within the data set would be preserved and the arch effect eliminated.

The choice of which technique of multivariate analysis to use must lie in the suitability of the method for the data set and whether it will answer the question that the researcher poses (Gauch, 1982). DECORANA has been devised specifically to cope with the samples by species style of data matrix used by ecologists, which relies on the same information structure as presented in palynological data. The results obtained through vegetation studies and from palaeoecological sources often generate a data set in which more than half of the values are zeros. Some techniques, e.g. P.C.A., cannot handle data satisfactorily in this form, but DECORANA is sufficiently robust to cope with data sets in which there are a high proportion of null values. The preservation of the relative ecological distances provided by DECORANA is an important requirement, and is crucial to the later interpretation of the data obtained in this study.

For these reasons DECORANA was the ordination technique chosen for this study.

4.5 CLASSIFICATION

Although classification techniques have been used by botanists for nearly 200 years (Whittaker, 1962), one of the earliest workers to group vegetation into classes, or noda, in order to produce a hierarchical classification was Braun-Blanquet (1932; 1951). This work was initially resisted by many botanists as being too artificial to be of widespread value. A critical review of this work by Poore (1955; 1956) resulted in a modified Zurich-Montpellier system which overcame many of the previous objections (Kershaw and Looney, 1985).

Classificatory systems are very convenient for they reflect the way we humans think (Goodall, 1953) and are therefore often easier to interpret than the gradients of continual variation produced by an ordination analysis. McVean and Ratcliffe (1962) noted that natural variation between vegetation communities was often continuous, and therefore, it was artificial to package them into separate units. This led to ordination being regarded as more 'scientific' than classification and many authors, e.g. Greig-Smith, recommended that the use of ordination should precede the use of classification.

Curtis (1959) showed how a classification analysis could be used to reduce a large data set to broad vegetation types, which were then used for an ordination analysis. Gauch and Whittaker (1981) suggested that classification and ordination techniques should be used together, with neither being given preference. In order to do this it was necessary to have compatible programs which would use the same data sets and have the same underlying constraints.

One program which was developed with this purpose in mind was Two-way Indicator Species Analysis, TWINSPAN, (Hill, 1979a; Gauch and Whittaker, 1981) which Gauch and Whittaker suggested should be used with DECORANA.

TWINSPAN is a polythetic divisive classification technique which is a refinement of 'Indicator Species Analysis' (Hill *et* al., 1975). In essence there are three ordinations within the program providing axes which are then divided to provide the classificatory units. The programme first ordinates the samples using RECIPROCAL AVERAGING. The samples at the extremes of the axes are emphasised in order to polarise the data set. The RECIPROCAL AVERAGING axis is then broken near its middle in order to obtain the first two groups. This sample division is then refined by a reclassification using species with a maximum indicator value. It is at this point that a species may be 'misclassified'. This categorises species which were so close to the point of division that the initial ordination placed them into one group whilst the reclassification transferred them into the other group. The process to obtain the first subsets is then repeated on each of the resultant groups until the divisions reach a user-defined limit.

Although quantitative data are used by the program, the method employed within the program is essentially qualitative. The quantitative data is converted within the programme to qualitative pseudospecies (Hill et al, 1975; Hill 1977) and in this way much of the quantitative information is retained (Hill, 1979a). Gauch and Whittaker (1981) compared TWINSPAN to four other classificatory techniques and found it to be the most robust when a data set is noisy, complex, large or unfamiliar.

TWINSPAN is an unconstrained classification technique: if used on fossil data it will group the most similar samples, no matter where they occur in the core. Whilst this is on occasion useful, there is also a use for a constrained classification to highlight significant changes in the biostratigraphy of the core.

Cushing (1967) was the first to apply objective criteria to determine the zonation of a pollen diagram. This concept was developed by Gordon and Birks (1972) who introduced POLZON, a package of programs which carried out three statistical tests to determine the placement of zone boundaries. The reader is referred to that paper for a full account of the statistics utilised; a brief summary is given below.

Constrained Single-Link Clustering, CONSLINK, measured the dissimilarity between all pairs of adjacent samples. The two stratigraphically adjacent samples with the lowest dissimilarity are then agglomerated and henceforth treated as one sample. The process is repeated until all pairs have been grouped together. The last pairs to agglomerate represent the most significant zone boundaries. This technique will pick out unusual levels as these will be amongst the last to amalgamate, this may lead to the definition of atypical levels rather than the zones of similar pollen types. Single-Link Clustering has been criticised as a technique for use with ecological data by Hill (1977) on the grounds that it produces straggly clusters which quickly agglomerate very dissimilar samples. This criticism would apply equally to Constrained Single-Link Clustering as the only modification is that only sequential pairs are considered.

The second POLZON analysis is SPLITINF which divides the data on the basis of its total information content to produce successive alternative groupings. This method is probably more reliable in its selection of zone boundaries than CONSLINK.

The third method SPLITSQ divides the data on the sum of least squares deviations. This provides a set of optimal groupings based on the minimisation of within group variance.

Within a pollen diagram there may be two types of biostratigraphic zones:

i) where there is a relatively stable pollen composition in each zone; and

ii) where these may be interspersed with intervals of abrupt change in the pollen spectrum.

(Walker, 1966, 1972; Watts, 1973).

Pollen zones will usually represent the first of these, and it is usually such zones of stability which are of interest to palynologists. However, periods of disturbance and rapid change reflected in the second type of pollen zone may also prove interesting. SPLITINF and SPLITSQ will tend to place zone boundaries in the middle of such a zone, particularly if only represented by a few levels (Gordon and Birks, 1974). Thus it is to be expected that the three different methods of data analysis used within POLZON will provide slightly differing but complementary results, although those of SPLITINF and SPLITSQ are more likely to be similar.

4.6 THE APPLICATION OF MULTIVARIATE ANALYSIS TECHNIQUES

4.6.1 Lamb's Procedure

Lamb (1984, 1985) presented a reconstruction of the Holocene vegetational history of Labrador through a multivariate analysis of the modern pollen rain input to moss polsters. Modern analogue sites were drawn from a variety of tundra habitats, to provide a basemap on which the fossil pollen spectra were subsequently superimposed. No vegetational analysis was carried out at the point of collection of the moss-polsters but the vegetation of each site could be broadly characterised according to the vegetation descriptions of such authors as Hare (1959) and Wilton (1965). The data were analysed using P.C.A. and axes 1 and 2 were plotted. This enabled Lamb to ring all the modern moss-polster sites originating from a similar habitat. This ring would then give a range of pollen representation for that habitat type and provide a base-map of vegetation zones.

A degree of overlap may occur between the site groups resulting from the Lamb procedure (1984, 1985). This phenomenon may result from the continuum of habitat types referred to by McVean and Ratcliffe (1962) or it may have been due to the inability of palynologists to determine pollen to a fine enough taxonomic level to separate some vegetation types. Overlapping might also be expected near the edge of a vegetation type, where the regional pollen component is contributing pollen from another habitat type. The component scores for the fossil data were then calculated independently and superimposed over the base-map (Lamb, 1984). Following the example of Gordon and Birks (1974), neighbouring levels in the core were joined by a straight line. In this way the line representing the changing vegetation communities could be seen to move over the vegetation base-map. Where the fossil points lay within the modern vegetation zones it was inferred that this was the predominant vegetation type prevailing at that time. Where the line lay outside the range of the modern analogue sites it was concluded that this represented a vegetation type which was not recorded amongst the modern pollen rain and may therefore have been an association which no longer exists in Labrador (Lamb, 1984).

The results of P.C.A. treated in this way present a detailed but rather confused picture which may be simplified by means of a final classification to obtain fossil pollen assemblage zones. Lamb (1984) achieved this using Minimum-Variance Cluster Analysis and Canonical Variates Analysis. The classification produced five groups, which could be located on the base-map by taking the mean P.C.A. co-ordinate of each axis for each group. The range of P.C.A. values in each group were shown by lines connecting the extreme values passing through the mean position. The five groups could then be joined, in geostratigraphic order, by a line. This then provided a summary diagram of the original P.C.A. output.

4.6.2 A Modified Procedure

This technique formed the basis for the statistical analysis of the palaeoecological data presented in the present study. As with any new technique refinements can be suggested. In the analytical sequence proposed here, DECORANA, TWINSPAN and POLZON were substituted for the three statistical techniques used by Lamb. Furthermore whereas Lamb relied on a rather generalised vegetation description for the definition of his vegetation zones, this study introduces a further statistical level, with a quantitative analysis of the vegetation surrounding each modern pollen site. A further change is that the modern and fossil data are combined into one matrix rather than Lamb's method, calculating the co-ordinates of the fossil points separately.

4.6.3 Development

The vegetation data for the ground flora were classified using TWINSPAN to obtain a vegetational framework. This resulted in the grouping of three main vegetation types: grasslands, wetlands and woodlands. The woodlands group could be further annotated using the TWINSPAN of the arboreal survey data to identify the dominant tree taxa. These data were completely independent of the ground flora data and thus any circularity in the argument was avoided.

The pollen traps were located in the centre of each vegetation survey area and therefore the results of the two data sets were directly related. However, as the values from the two analyses were not expressed in a comparable form, they could not be entered into a single data matrix.

The DECORANA ordination produced values for each site on 4 axes. These could then be plotted, the scale of units being provided by the average standard deviation of species turnover x 100 (Hill, 1979b). Generally it was the first two axes which were the most interpretable. The modern analogue points could be ringed so as to group all the points from locations defined by the TWINSPAN analysis as having similar vegetation communities. This provided the same style of vegetation base-map as obtained by Lamb (1984). The difference was that the base-map utilised in this survey was precisely related to a detailed inventory of the local flora.

Where a fossil data matrix and a modern analogue data matrix were combined, and the DECORANA output plotted, the modern analogue points could be circled as described above. The fossil points could be joined in stratigraphic sequence as in the method proposed by Lamb (1984). As in Lamb's procedure it was possible to simplify the diagram and to produce a summary diagram based on a final classification of the fossil points.

4.7 THE COMBINATION OF MODERN ANALOGUE AND FOSSIL MATRICES

For DECORANA to be used in the method described above it was necessary to combine the fossil and modern analogue data matrices.

If two matrices are to be amalgamated, then they must be totally compatible, that is they must be derived from an identical method of measuring the same variable. For pollen samples the laboratory methods should be as nearly identical as possible, the identification of pollen must be consistent and count sizes should be comparable. Dimbleby (1957) suggested that if only the commoner taxa are to be used the actual count size is less critical. Those species which make up the sum must also be consistent between the data sets to be joined.

If these criteria are met then the two matrices may be combined and analysed as one data set. These criteria were met for the modern and fossil samples in the macrofossil, pollen and mollusc data sets. The matrices of modern and fossil pollen were combined, as were the data for modern and fossil fruits, and for modern and fossil molluscs.

4.8 PSEUDOSPECIES

In this study the use of a semi-quantitative technique with the TWINSPAN analysis is a positive advantage as there may have been errors in almost every level of palaeoecological preparation. This may have taken the form of the loss of pollen during processing, or in the uneven distribution of pollen on a slide, or simply the confidence limits that could be placed on the totals from any pollen count. It was therefore advantageous to have a system in which it was broad differences which were sought, rather than variations in fine detail. The pseudospecies cut-levels were defined by the user, although a default set was provided for use with percentage data; this was: 0, 2, 5, 10, 20 (Hill, 1979a). The pseudospecies may be weighted, although default weightings of 1, 1, 1, 1, 1, were provided. In this study, where percentage data were used, the default values for both the weightings and the cut-levels were accepted.

The vegetation survey data, as stated earlier, contained a degree of error for dense vegetation types, e.g. tussocks. The survey would however have been sufficiently accurate to allow the confident placement of these values into the relevant pseudospecies. As these data were analysed in their absolute form new cut-levels and weightings were applied (Table 4.4).

GROUND FLORA CUT-LEVELS	WEIGHTING
0 - 100	1
101 - 200	1
201 - 400	1
401 - 800	1
801 - 1600	2
1601 - 3200	2
3201 - 6400	2
> 6400	2

ARBOREAL CUT-LEVELS	WEIGHTING
0 - 50	1
51 - 100	1
101 - 500	1
501 - 1000	1
1001 - 5000	1
> 5000	1

Table 4.4 Vegetation survey data pseudospecies weightings

Various patterns of cut-levels were tried and it was found that there was little to choose between them in terms of the clarity of the analysis. The cut-levels shown above provided the most readily interpretable axes and so they were adopted. The cut-levels selected for the ground flora analysis had the effect of increasing the importance of the most abundant taxa and reduced the chance that the data might be distorted by rare taxa or statistical 'outliers'. The logarithmic scaling of the arboreal data cut-levels performed a similar function.

4.9 CONSTRUCTION OF MATRICES FOR MULTIVARIATE ANALYSIS

A feature of DECORANA is that if required rare species can be downweighted. This effectively reduces the significance of rare species within the data set but does not exclude them from the calculation. The use of downweighting is appropriate where the data set contains outliers which may distort the ordination

(Gauch, 1982).

Although DECORANA is designed to handle rare species it is not designed to handle species which do not belong to the principal habitat(s) which are featured in the data set. It is also recognised that an ordination will be stronger if there are few outliers in the original data set (Gauch, 1982).

a) pollen

In order to overcome the problem of rare or of long range pollen types distorting the data set it was decided to exclude the rarest taxa. This is not novel but it would seem that there is no general rule about which taxa are to be excluded. Birks (1973) excluded those taxa which did not attain 5% of the total pollen and spore count in at least one sample, whereas Lamb (1984) excluded those that were not present in at least 6 out of 71 samples, or failed to attain values greater than 2% of the dry land pollen total.

In the data set obtained from this study species which occurred at less than 5% dry land pollen included many species which were strong environmental indicators, or species which had a distinctive distribution, but a low representation in the pollen data. To adopt the method used by Lamb (1984) did not exclude enough taxa and so it was decided to exclude any taxa which did not exceed 5% of the total dry land pollen unless they were present in 5 consecutive samples. After an initial ordination further exclusions were made. These were: Pinus, aquatic pollen taxa and all spore taxa.

This approach is justified on the grounds that all these taxa can distort a data set. Pinus pollen can be derived by secondary deposition from glacial tills (Suggate and West, 1959). It is a pollen type which can be transported long distances and attain values as high as 60% when the nearest occurrence of the tree is over 300 km distant (Ritchie, 1974, Ritchie and Lichti-Federova, 1977). Furthermore, in recent times it has been widely planted by man. Hence the occurrence of Pinus in a data set such as this must be viewed carefully, and does not necessarily indicate specific environmental conditions. For similar reasons Howe and Webb (1983) excluded Ambrosia pollen from their statistical analysis. Aquatic taxa and spores are commonly excluded from calculations on the grounds that they are subject to strong local over- representation, which may or may not have any ecological significance. It is best that these taxa are excluded from the pollen analysis and instead, the local emphasis will be provided by the macrofossil analysis.

The fossil pollen matrix which was used for all subsequent DECORANA analyses consisted of 43 species, reduced from a total of 132, occurring in 60 samples.

The data matrix for the modern pollen samples automatically included all the taxa used in the fossil pollen matrix. In addition to this any species occurring at a level of greater than 5% was also included. As the two matrices were compatible they were first run independently and then combined to form a single matrix of 94 sites and 47 taxa.

A further six samples were added from the data provided in Birks (1973) to the combined modern and fossil matrix to extend the range of sites offered by the modern analogues. The same criteria for selection of species were utilised to ensure data compatability.

The statistical analysis of the Gramineae pollen size data is reviewed separately in section 4.11

b) macrofossils

Most plant propagules would have been derived from within 5 m of the sampling point (Ryvarden, 1971a,b; GreatRex, 1983). Additionally there would have been less likelihood of a purely random long range seed input than amongst a pollen component. Long range dispersal of seeds and fruits can take place, especially when the vector is an animal; however the proportion of seeds introduced in this manner from a remote and unrelated habitat is likely to be very small. The macrofossil data are therefore likely to have fewer misleading outliers than the pollen data set. For this reason the entire seed data set, expressed as a percentage of the total propagule count, was utilised for the DECORANA analysis. This was also the case with the data for mollusca, where the entire data set, expressed as a percentage of total molluscs, was used for the statistical analyses. In both instances a DECORANA and TWINSPAN analysis was run on the modern and fossil assemblages separately before the matrices were combined.

4.9.1 Data Transformation and Downweighting for the DECORANA Analyses

The three pollen matrices were run with and without the downweighting of rare species. In each case the results of the analysis without downweighting proved to have higher eigenvalues for each axis and the first two axes were more easily interpretable. The macrofossil data sets were also found to yield the most interpretable results without downweighting.

The analysis of the arboreal vegetation data set was run on the absolute values for the weighted canopy area with and without downweighting. It was found that the results were readily interpretable without needing to downweight or change the scales of abundance. The default values were, therefore, accepted for this analysis. The ground flora data were transformed to a scale of abundance from 1 - 8 using a logarithmic scale (Table 4.5).

GROUND FLORA ABUNDANCE VALUE	TRANSFORMED VALUE
0 - 2.7	1
2.8 - 8.0	2
8.1 - 27.0	3
27.1 - 80.0	4
80.1 - 270.0	5
270.1 - 800.0	6
800.1 - 2700.0	7
2700.1 - 8000.0	8

Table 4.5 Transformation of ground flora abundance values for the DECORANA analysis

This was done to reduce the effect of any measurement error when dealing with dense stands of fine-leaved vegetation. The loss in sensitivity from this transformation did not appear to be reflected in the output, the first two axes of which were readily interpretable.

4.9.2 The POLZON Matrices

The data set required for POLZON was necessarily different from that used for the other statistical analyses because of the limited matrix size available for use with this program. The limits were 18 taxa and 80 levels. This meant reducing the number of pollen taxa from 43 to 18 and the number of propagule taxa from 115 to 18. Key taxa could have been selected, or there could have been an amalgamation of taxa into groups such as trees, shrubs etc., or thirdly, there could have been a combination of these measures. As so much information would have been lost through the two former methods it was decided subjectively to include certain key taxa (all of which were present at greater than 10% of the total) and to divide the remainder into broad ecological groups. This had the effect of reducing the number of rare species and so making a smoother data set. Whilst this method might be criticised for the loss of sensitivity and subjective selection of taxa, the results of the unconstrained classification technique, TWINSPAN, run on the data set in which 43 taxa were utilised, provided very similar results (see Table 8.1). This would suggest that the shrinkage of the data set to the 18 'key' categories did not materially reduce the reliability of the classification.

For the POLZON analysis of pollen data these were:

'cold' or 'montane' herbs, e.g.	*Gentiana* spp., *Armeria*, *Polygonum viviparum*, *Saxifraga*
'cold' or 'montane' shrubs, e.g.	*Empetrum nigrum*, *Betula nana* *Arctostaphyllos*
grassland, e.g.	*Achillea*, *Sanguisorba minor* *Helianthemum*, *Linum*, *Gentianella*
fen, e.g.	*Menyanthes*, *Potentilla* *Polemonium*
aquatic, e.g.	*Myriophyllum* spp., *Typha* spp., *Alisma*, *Potamogeton*
arable, e.g.	*Centaurea cyanus*, *Chenopodium*, *Aphanes*
pastoral, e.g.	*Rumex*, *Urtica*, *Bellis*, *Plantago lanceolata*.

In addition to these the following individual taxa were included: *Betula*, *Quercus*, *Corylus*, *Alnus*, *Salix*, Gramineae, *Filipendula*, Cruciferae, Cyperaceae and *Equisetum*. These were not double counted by also including them in the aggregate totals. Taxa which could not be ascribed with any certainty to a particular group were excluded from the analysis. These included: *Ranunculus*, *Cirsium*, *Epilobium* and *Heracleum*.

For the propagules a similar grouping was carried out resulting in the categories: 'cold' or 'montane' shrubs, grassland, disturbed ground species, fen and, lastly, aquatic taxa. There were also the individual taxa: Alnus, Betula, Salix, Stellaria media, Urtica dioica, Menyanthes trifoliata and Cyperaceae. As with the pollen, data for Ranunculus sec Ranuculus, Cirsium and Epilobium were not included in the calculations.

For molluscs the species were divided into obligate aquatics, obligate hygrophiles, woodland taxa, open ground taxa and catholic species. No individual species scores were utilised.

4.10 A COMPARISON OF THE TECHNIQUES USED TO COMPARE MODERN AND FOSSIL DATA

Modern pollen rain is generally used by palaeoecologists in one of four ways. These are:

i) to provide an indication of the present pollen input to the site for semi-quantitative uses, e.g. estimating the importance of the relative components of wetland, arboreal and non-arboreal taxa. For this sort of study a few moss polsters from the site being studied are collected and analysed.

ii) To estimate the specific input of various taxa. This has been applied in woodlands to obtain R-rel data for use in assessing the relative proportions of the arboreal pollen input (Andersen, 1970, 1973; Bradshaw, 1981a). For this type of study large numbers of moss polsters, or pollen traps, are required, from diverse locations.

iii) To estimate the proportions of pollen derived from different sources and distances (Tauber, 1965; Jacobson and Bradshaw, 1981; Janssen, 1984; Prentice, 1985) and to estimate experimentally the proportion of water-borne pollen incorporated into a sediment (Peck, 1973; Bonny, 1976; Pennington, 1979). This work relies heavily on the use of various designs of pollen trap, although for some experiments moss polsters are used.

iv) To compare a range of modern analogue sites from known vegetation communities with the fossil pollen record in order to obtain a forest history related to the range of the modern analogues (Lamb, 1984, 1985; Bradshaw and Webb, 1985).

The techniques used in the present study allowed the comparison of the results of three of these forms of data analysis. Moss polsters were collected from Willow Garth to establish the modern pollen rain to that site. All that this can be used for is to assess whether the past environment was different from that of the present day.

R-rel values were calculated and the data obtained applied to the fossil data set to obtain the relative canopy proportions of past environments. The analysis of the local vegetation, the modern pollen representation of that vegetation and the fossil pollen record were utilised to obtain a history of the vegetation relative to the modern analogue plots.

As the results from the two latter methods were quite different it may be profitable to compare the models they rely on.

4.10.1 R-rel

The use of R-rel weighting values has the capacity to depict accurately the composition of a forest canopy based on its pollen yield. The over- or under-representation of species is taken into account and the absolute pollen count is weighted accordingly. For an accurate result to be obtained with fossil data stringent criteria, which underpin the model, must be fulfilled:

i) That the past pollen deposition of trees was the same as it is today and that their ecological requirements have not changed.

ii) That there was no selective redeposition of material within the fossil sediment after the time of deposition.

iii) The pollen caught in the traps was derived from a uniform distance for all the species, i.e. either all species are equally effective at distributing their pollen, or that the plot chosen to represent the woodland is part of a homogeneous woodland.

iv) The radius of the study plot provides the spatial limit over which conclusions regarding the fossil forest can be made, i.e. if the radius of the study plot is 20 m then if the forest of the fossil samples lies at a distance of more than 20 m the comparison is invalid.

v) That the fossil sampling point was as equally representative of a homogeneous forest as the point of modern pollen collection.

vi) That it was an arboreal environment represented in the fossil record.

vii) That there are no errors of measurement.

The first two of these criteria apply to all modern analogue sampling techniques. The selective redeposition of pollen is a problem inherent in peat-bogs (Rowley and Rowley, 1956) and also in lakes (Davis et al., 1971). However, this problem is believed to be of minor significance and does not present a problem in all deposits (Davis et al., 1971). The pollen production of past trees is not known but it is assumed that anther and flower structure has remained constant for most species during the Quaternary and that their pollen production would be similar to that of the present day. The associations of plants in fossil spectra are broadly similar to those found today and where discrepancies occur this is generally attributed to the interference of man rather than a change in habitat requirement.

The third criterion can be met in some forest environments, e.g. in dense pine or birch woods, or other monotypic stands where one is certain of the homogeneity of the forest. Otherwise it is unlikely that any natural woodland will be truly homogeneous. It is well known that some species will disperse pollen over many kilometres, e.g. Quercus, whereas the pollen of others such as Fagus and Acer will travel relatively short distances (Bradshaw and Webb, 1985).

The measurement of girth at breast height (gbh) can be made exactly, although coppiced stools present problems in this respect; error can also be introduced by measuring immature, diseased or senescent trunks. Gbh however is not a direct measure of the flower production of a tree. To measure the canopy area of a tree is a more direct assessment of the flower bearing portions of a tree but it is time-consuming and is equally uncertain of total accuracy. That notwithstanding, it was found to provide the best correlation with pollen production in the woodlands surveyed in this study.

As the fossil forest must have occurred within the sampled distance of the fossil site this technique is only applicable to small hollows within woodlands. Given that a wet hollow is an atypical habitat within a dry-land woodland, it is unlikely that the trees surrounding the hollow are going to represent a homogeneous habitat. Some taxa, e.g. Salix and Alnus, may be obvious in having a wetland distribution and therefore candidates for exclusion from the pollen sum; but what of other taxa which are known to show a preference for moist ground, e.g. Tilia ?

4.10.2 Statistical Comparison of Modern and Fossil Pollen Data

The product of this comparison does not provide the exact accuracy of R-rel values, but the criteria which the model relies on are less stringent and ecologically more realistic. The first two criteria of the above list are part of this model and in addition to these there is the single criterion that:

iii) modern analogues exist to cover the range of past environments.

This has been challenged by Behre (1981) who asserted that there is no modern equivalent of the prehistoric farming landscapes of the Bronze Age and Iron Age. This was also a problem encountered by Lamb (1984) in that even in the relatively virgin territories of arctic Labrador he found that many of his fossil samples lay outside the range of the modern analogues. A site as exceptional as Willow Garth is unlikely to have an exact modern counterpart, for there are no such fen swamps on the chalklands today. Exact analogues may not be necessary, as long as there is a sufficient range of modern data points that the fossil sites fall within them.

One outstanding virtue of the modern analogue system is that its use is not restricted to pollen or indeed to plants, but can be used on any ecological information where there is sufficient quantitative information available. The rate of change of different groups in response to an environmental change can be monitored and it greatly enhances the comparison of different data sets. This was utilised in the current study to show the timing of major habitat changes on a local and a regional scale.

4.11 STASTICAL METHODS APPLIED TO THE GRAMINEAE POLLEN SIZE DATA

The percentage of each size class was calculated as a total of the Gramineae recorded in that sample; this was repeated for each level in the core. The greatest advantage of using Gramineae pollen size percentage data is that they offer a data set entirely independent of any of the other data sets. In the data matrix the size classes become the equivalent of species, and the data set could be statistically treated using DECORANA, TWINSPAN and POLZON. If each size class is treated as a separate species this is highly artificial, as a size range is a continuum and not a series of separate units. By regarding each size unit in this way information is lost, but the loss of information does not invalidate the use of the statistics. Indeed it may be likened to a statistical analysis which includes species such as Alnus and Salix as separate taxa. These species will often grow together and have very similar ecological requirements, and so it could be argued they are not ecologically totally unrelated. The computer can make no allowance for known relationships and so would weight a difference between any two taxa equally. In this way information is lost in any analysis but it does not invalidate the statistics.

POLZON was used to define the levels at which a marked change in the size categories took place. TWINSPAN was used to determine levels which showed a similar size distribution to levels from other points in the core, without the sequential constraints imposed by POLZON. DECORANA was utilised to compare the clustering of samples and the ecological distances between the samples. The results of the Gramineae data DECORANA analysis could be compared with those of the ordination of fossil pollen and fossil propagule data.

Through the use of these techniques it was hoped to establish whether the variation in size distribution was synchronous with local (macrofossil) or regional (pollen) vegetation changes. This would give some indication as to whether the grass pollen was of local or regional origin.

The 18 size classes used for POLZON were:

<20, 21 - 22, 23 - 24,......52 - 53, >54 μm

Before deciding on the size categories to be used in the

DECORANA and TWINSPAN analyses it was necessary to frame the question to be answered by the statistical analysis. In this case it was to decide whether the ecological distances between Gramineae pollen samples mirrored those of the overall pollen input or the propagule input. To include a full record of the various large-sized Gramineae pollen for analysis would be to provide a large pool of potential outliers as they are all relatively rare groups. The program would treat them as ecologically distinct categories, whereas their principle ecological value is to indicate that man had undertaken arable farming. At that size they were almost certain to be Cerealia, as even the largest of the wild grasses were not recorded to exceed 52 µm (Beug, 1961). It was decided, therefore, that the size categories used for the POLZON analysis should be retained for the DECORANA and TWINSPAN analyses.

CHAPTER 5: THE MODERN ANALOGUE SURVEY

5.1 MODERN ANALOGUES: THE RATIONALE

In this chapter the results of a modern analogue survey, an approach which has been well reviewed by Wright (1967), are given. Modern analogues were drawn from a wide variety of contemporary calcareous habitats in order to provide a range of type assemblages from known habitats and, as importantly, to obtain an impression of the range of variability in the pollen, plant propagule and mollusc record from within each major habitat type. If a wide variety of habitats are sampled it is hoped they will encompass the range of habitat variation found within the fossil samples. This will enable the fossil data to be compared with the modern analogue sites at a community or assemblage level. This is not aimed to replace the use of indicator species to yield accurate climatic information but as a complimentary tool for use in the interpretation of fossil data. The major habitats utilised are given below and there then follows a description of each modern analogue location prior to reviewing the results. The actual location of analogue sites rested on a number of criteria. These were:

1) To obtain data from a wide variety of habitats.

2) There should be a roughly even numerical proportion of samples from each major vegetation type.

3) The samples should be drawn from natural or semi-natural vegetation communities as these are most likely to mirror past communities.

4) The site should be relatively undisturbed and

unfrequented by man to minimise loss of pollen traps left in the field for one year.

In practice the best sites were often nature reserves or S.S.S.I.'s. However, some habitat types, believed to be potentially important analogues, were not available on the Yorkshire Wolds. In these cases analogues were drawn from other calcareous regions wherever possible.

5.2 THE MAJOR VEGETATION ASSOCIATIONS OF THE YORKSHIRE WOLDS

5.2.1 Grasslands

The grasslands of the British chalklands have been described in great detail by Tansley and Adamson (1926), Tansley (1939), Hope-Simpson (1941b), Thomas et al. (1957) and Shimwell (1971ab). For a full account of the floral structure of these grasslands see the works listed above. In terms of the European vegetation classification most of the chalk grasslands of the north of England would be placed in the Festuco-Brometea alliance (Shimwell, 1971ab).

The British chalk grasslands have been shaped by centuries of grazing. The resultant sward depends on the intensity and type of grazing pressure to which it has been subjected, i.e. cattle are coarse grazers, whereas sheep will crop more selectively. Where there is a high grazing intensity, sheep will produce short, evenly cropped turf; whereas cattle produce a patchwork effect of tufts and closely grazed grassland (Wells, 1969).

Grazing animals will trample the vegetation. This might lead to areas of local erosion (McAndrews, 1966), providing a niche for the colonisers of bare ground. The meadows will also be enriched by the dung and urine of the grazing herbivores. This will not be uniformly distributed as there will be higher concentrations in sheltered areas, along routes taken into, or out of, the feeding area, or where animals go to water. Thus a grazed grassland sward is seldom homogeneous.

If a grassland is occasionally grazed, or if it is grazed irregularly by different animals, with different styles of grazing, then perennial plants are likely to maintain a relatively constant population, whilst annual plants may fluctuate wildly in number from year to year (Wells, 1969).

5.2.2. Chalkland Fens

Whilst there are many fens near the chalk outcrop there are very few which actually overlie the chalk. Using the European method of habitat classification Wheeler (1980b) placed a spring-fed fen at Great Driffield (just off the chalk) into the Acrocladio- Caricetum subassociation juncetosum.

Water, rich in calcium carbonate and mineral nutrients derived from the chalk, drains off the Wolds into the River Hull. Fens in the Hull Valley, e.g. Pulfin Bog and the now drained Leven and Eske Carrs, were maintained as base-rich flood meadows by the winter overtopping of the River Hull. The fen community at Pulfin Bog was placed in the Peucedano-Phragmitetum by Wheeler (1980a). Wheeler did not describe any of the fen communities from the spring line along the scarp (western) slope of the Wolds, although these are the commonest and most floristically diverse of the fens on or near the Wolds at present.

5.2.3. Woodlands

Whilst an extensive European strategy for woodland classification has been established (e.g. Klotzli, 1970) and has occasionally been utilised to classify British woodlands, (e.g. McVean and Ratcliffe, 1962) the European classification does not provide an adequate system to describe British woodlands. As Rackham stated :

> "In practice, the farther one travels from Zurich or Montpellier, the less convincing does the hierarchical classification appropriate to Central European vegetation become."
>
> (Rackham, 1983. p. 659)

A first step towards categorising our native woodlands was to identify which were the ancient woodlands and which were the planted or heavily managed woodlands. Rackham (1980) provided an excellent guide to the recognition of ancient woodlands using ground flora indicator species. Working independently, Peterken (1981) identified ground flora assemblages characteristic of a broad variety of woodland types, a list which was in broad agreement with that of Rackham (1980).

Peterken (1981) went on to develop a classification of British semi-natural woodlands aimed to be sufficiently robust to be used with a minimum of quantitative data. The data utilised by

Peterken were drawn from 700, 30 x 30 m quadrats in semi-natural woodlands throughout Britain (Peterken, 1981 Fig. 7.2). From these a classification was established in which 12 basic stand types and 57 sub-types or variants were recognised. The criteria for separating stand types relied on combinations of species present in the canopy, understorey and ground flora. The physical properties of the site were also considered, specifically: topography, the soil pH and texture at 10 cm depth. In some instances the absence of certain species from an assemblage was an additional indicator as to the classificatory group. This classification gives rise to such groups as :

Stand type 9B. Sessile oak - hornbeam woods

Sub-type 9Bb. Calcareous sessile oak - hornbeam woods.

Although this work did not deal specifically with any of the woodlands on the northern chalklands the classification provided by Peterken (1981) is applicable in many cases.

5.2.4. Edge Habitats

At the divide between two vegetational communities there is frequently a zone characteristic of neither and yet, containing a high proportion of the flora and fauna of both. Such an ecological edge will contain a more diverse flora and fauna than is contained in either of the two 'pure' stand types. The species growing at the edge will not be the rarest, or the most sensitive species, but they will tend to be the generalist members of each association.

Edge effects are of great importance in palaeoecology, as the site of deposition, usually being wet, would have such an edge between it and the dry land habitats. The herb species represented in the transitional area, from open water to dry ground, or from fen to forest, are those dry land species most likely to be incorporated into a fossil deposit. This is because they are the closest to the depositional site and are not separated from the site by a screen of trees.

These woodland fringes are the areas which early settlers were most likely to influence (Simmons et al., 1981; Edwards, 1982). Equally, the majority of archaeological sites used for palaeoecology would be, by definition, providing data from a disturbed environment, i.e. in which there has been clearance or draining to produce an 'unnatural' assemblage of species. This would present a fossil association which would have many similarities with an association derived from a natural edge population.

Whereas phytosociologists ignore these areas as being atypical of a vegetation association, they are in fact the associations which palaeoecologists are most frequently dealing with. Therefore, it may be advantageous to establish modern analogues for such habitats so that they may be recognised in the fossil pollen data.

5.3 SITE DESCRIPTION OF MODERN ANALOGUE STUDY AREAS

5.3.1 Flamborough Head (Ordnance Survey grid ref. TA 143764 - 195682)

The cliffs around Flamborough head form a linear nature reserve and a long distance footpath runs along the clifftop. Although constantly disturbed by erosion the grasslands on the shallower slopes of the cliffs bear a rich chalk grassland flora, e.g. Armeria maritima, Plantago maritima andAnthyllis vulneraria. Where slippage has resulted in fens forming, Parnassia palustris, Dactylorhiza purpurea and Glaux maritima may be found. There are no trees on the headland and the closest woodland is more than 2 km distant. This area is designated an S.S.S.I. on geological grounds, but is nevertheless heavily disturbed by visitors.

Six pollen traps were placed in the quieter, or more inaccessable areas on the cliffs around the South Landing. One was placed in a clump of gorse and bramble, two were placed on steep grasslands rich in Primula vulgaris and Cochlearia officinalis, two were placed in spring flushes and one on a shallowly shelving old slip surface covered in grassland species such as Sanguisorba minor and Plantago coronopus. Of these, two were recovered, one from the gorse clump and the other from a precipitous north-east facing grass sward. The others were probably lost to a mixture of cliff-slumping and human interference.

5.3.2 Kiplingcotes Chalk Pit (Ordnance Survey grid ref. SE 915435)

Kiplingcotes Chalk Pit is a 3 ha revegetated chalk quarry, which, since 1965, has been managed as a nature resevre by the Yorkshire Wildlife Trust. The quarry provided materials for the construction of the railway line which, now disused, bounds the reserve to the south.

Approximately 160 species of vascular plants have been recorded from the reserve including: *Scabiosa columbaria*, *Centaurea scabiosa*, *Anacamptis pyramidalis* and *Gentianella amarella*. *Brachypodium pinnatum* threatens to overrun part of the reserve and despite efforts to control this species by cutting and fire some of the grassland areas are now species poor as a result of the invasive growth of this grass. The landscape around the reserve is predominantly agricultural and there are very few trees in the valley.

Four pollen traps were set in the valley bottom amongst the short herb rich sward and four more were set in taller grassland communities to the side of the main quarry area. Of the eight traps, all those in the valley bottom were lost to freak winter flooding, one placed in the taller grassland community was burnt and another though collected intact came from an area of grassland which was burnt before the vegetation survey had been carried out. The two remaining traps which had both been set amongst the species poor *Brachypodium pinnatum* grassland were recovered without mishap.

5.3.3 Fordon Chalk Bank (Ordnance Survey grid ref. TA 057751)

Fordon Chalk Bank is an 11.8 hectare area of mature chalk grassland, an S.S.S.I. established in 1975, which is now managed by the Yorkshire Wildlife Trust. This grassland has been listed as being a site of national biological conservation importance (Ratcliffe, 1977).

One of a disjunct series of grasslands in the chalk valleys around the village of Fordon, Eastdale or Fordon Chalk Bank, lies on the south facing side of a dry valley. The common grasses of this reserve are Festuca spp., Anthoxanthum odoratum, Briza media and some coarser grasses, e.g. Bromus erectus and Dactylis glomerata. This area is extremely diverse botanically, with an abundance of characteristic calcicole herbs such as Campanula glomerata, Carlina vulgaris, Filipendula vulgaris, Helianthemum sp., Sanguisorba minor, Blackstonia perfoliata and Geranium sanguineum. The hillside also supports scattered stands of Crataegus monogyna and Ulex europaeus. In the centre of the grassland these shrubs, plus Sambucus nigra, flank a small copse of Fraxinus excelsior.

Nine pollen traps were set in a variety of habitats within the grassland, five of them to collect the pollen production of the various communities within the short herb-rich sward. Three of these were recovered. Of the others, one in the edge vegetation surrounding the F. excelsior copse and one in the middle of a clump of gorse were recovered intact. Thus five of the original nine traps were of further use.

5.3.4 Kiplingcotes Spring (Ordnance Survey grid ref. SE 898426)

A deep hollow containing a spring lies between the road and the disused railway line from Market Weighton to Cherry Burton, (Plate 3). The hollow which is approximately 50 m across at the top narrows to a flat floor c. 20 m^2. This feature was probably created as another chalk pit to provide stone for theconstruction of the railway, and therefore is of a similar age to the Kiplincotes Chalk Pit which lies c. 1 km further down the valley.

To the south, east and west the sides of the spring hollow are steep grassland banks (c. 25°) with scattered hawthorn. A mature hedge of hawthorn and elder separates the eastern edge of the grassland from a field of 'improved' pasture. To the north of the hollow there is the outlet stream from the spring. The stream winds out through a small copse of Salix fragilis to join a larger spring fed stream which runs at the foot of the old railway embankment. The total area covered by the fen and the copse would be c. 0.5 ha. A seasonal pool lies in the bottom of the hollow, drying up from about June until September of most years. On drying a thin sandy sediment is uncovered; Apium nodiflorum, Berula erecta and Rumex conglomeratus grow in scattered clumps leaving most of the bed of the pool bare. When the depression is water-filled a pond up to 40 cm deep will form and this, particularly in early summer, often supports a dense algal growth.

The margins of the pool are sharp on the southern and western sides where the vegetation is dominated by tall herb communities such as Epilobium hirsutum, Pulicaria dysenterica, Scrophularia aquatica, Urtica dioica and Rumex spp.. On the eastern side the pool margin shelves slightly and a poor fen flora has developed containing U. dioica, Potentilla palustris, Ranunculus spp., and Carex spp..

Beneath the dense shade of Salix fragilis the ground flora is relatively sparse. Myosotis sp., and Berula erecta growing in the wetter locations, are the commonest plants; a few tufts of grasses occur but these are isolated and scarce. The Gramineae on the bank and in the unimproved pasture immediately surrounding the spring are tall as there is little grazing pressure, although some rabbits are present in the hollow. Festuca ovina, Dactylis glomerata and Phleum pratense are some of the commonest grasses of this association. The grassland is poor in broad leaved forbs, containing only Heracleum sphondylium and Centaurea nigra in any numbers.

Six traps were left in the marginal vegetation around the pool, five in the open area and one beneath the willows. All were recovered.

5.3.5 Pulfin Bog (Ordnance Survey grid ref. TA 052438)

Pulfin Bog is a 17 ha wetland nature reserve owned by the Yorkshire Wildlife Trust. It lies within a bend of the River Hull, which is still tidal at this point. The fen is a remnant of a series of wetlands in the Hull valley which included the Eske and Leven carrs, both of which have now been drained. Seasonal flushing by the calcareous waters of the River Hull occurs in

PLATE 3 THE SEASONAL POOL AT KIPLINGCOTES SPRING
(MARCH 1983).

winter, which has resulted in the formation of a fen dominated by *Phragmites australis* and *Glyceria maxima*. *Salix cinerea*, which grows in clumps around blowholes, of which there are five large ones, is the only tree which grows on the reserve. The fen vegetation is not grazed, and so is dominated by the tall grasses and a few resilient herb species e.g. *Filipendula ulmaria*, *Lysimachia vulgaris*, *Lythrum salicaria*, and *Valeriana officinalis*. At the northern end of the reserve is an inlet from the River Hull which contains *Stratiotes aloides* and *Phragmites australis*. Around the western edge of this embayment there are shallow pools which contain a more diverse wetland flora with such species as: *Juncus effusus*, *Angelica sylvestris*, *Potentilla palustris*, *Rhinanthus minor* and *Carex* spp..

Three pollen traps were left in the *Phragmites australis* and the *Glyceria maxima* stands, and a further three around the embayment from the River Hull. The only trap to survive was one in the embayment; the others were probably lost due to flooding.

5.3.6 North Newbald Fen (Ordnance Survey grid ref. SE 917372)

Springs rising along the dipslope of the Wolds often create flushes of fen vegetation. At North Newbald at least five springs rise within one short length of a gently falling valley. The permanence of these springs has resulted in the development of a rich fen flora. The fen is commonland, occasionally grazed by geese and swine, but not by cattle or sheep. Large *Salix* sp. dominate the eastern (upvalley) fringe of the fen and 300 m away at the western finge of the fen there is a stand of *Fraxinus* *excelsior* growing on a mound.

To the south, above the spring-line, arable fields form the boundary of the fen, and on the other valley side, some 70 m away, delimiting the northern margin of the fen, lies the road between North Newbald and Beverley.

In midsummer the vegetation is a rank growth of tall herb species such as *Filipendula ulmaria*, *Epilobium hirsutum* and, in the wettest areas, *Pulicaria dysenterica*. In the spring and early summer a much greater species diversity is apparent with species such as *Parnassia palustris*, *Caltha palustris*, *Cardamine pratensis*, *Menyanthes trifoliata*, *Geum rivale* and three species of orchid. The sedge *Carex ovalis* is the commonest member of the Cyperaceae although *C. panicea* and *C. hirta* are also present. *Juncus effusus* and *J. inflexus* form clumps on the edges of the spring flows but Juncaceae are otherwise scarce. The Gramineae are mostly fine leaved species such as *Festuca rubra* and *F. ovina* but *Poa* spp. and *Agrostis tenuis* are also common.

Where the spring water drains from the fen it runs into a canalised stream which contains *Mentha aquatica*, *Nasturtium aquaticum* and *Veronica beccabunga*.

The fen had formed an organic deposit which was investigated using a Hiller borer, but as the deposit was less than 30 cm deep the study was not pursued.

Five pollen traps were set within the fen: three were lost due to flooding or vandalism, the other two were recovered intact.

5.3.7 Wharram Percy (Ordnance Survey grid ref. SE 855645)

The mediaeval village of Wharram Percy was abandoned in the fifteenth century (Hurst, 1979) after which time the village pond, formed by the damming of a spring fed stream, silted up. The excavation of the pond in 1981 had laid bare the mediaeval dams and the silts which they had trapped. Samples for pollen analysis were collected from these sediments (Appendix 2). Shortly after this the valley bottom was once again flooded when the land owner, Lord Middleton, created a new dam on the same site as the mediaeval dams.

A rich fen had existed in the valley bottom prior to the flooding, but little survived the recent landscaping. However some stands of Juncus articulatus, J. inflexus and J. effusus. are still present around the margin of the pool. Above the pool lie the steep valley slopes which are a mixture of improved and unimproved chalk grassland. In the unimproved areas there is a close-cropped herb-rich sward which includes: Linum catharticum, Torilis japonica, Campanula rotundifolia and Sanguisorba minor. In the improved grasslands Lolium spp. are the dominant grasses, and Galium verum and Ranunculus acris are almost the only forbs to survive in this depauperate community.

In a meadow sloping down from the church there is ungrazed vegetation and here tall grasses, Centaurea nigra and Heracleum sphondylium grow in profusion. At the base of this meadow flows a stream in which Apium nodiflorum is the commonest plant. Glyceria plicata was also common in the stream prior to the construction of the new dam, although it was not recorded in this most recent survey. Along the banks of the stream grow Caltha palustris, Epilobium hirsutum, Filipendula ulmaria, Urticadioica, Pulicaria dysenterica, Mentha aquatica and Nasturtium aquaticum, forming the familiar tall herb community of the Wolds wetlands.

Of the six pollen traps set in the various habitats described only one survived. This one was sited downstream of the dam at the base of the improved grassland beside the stream, and opposite the ungrazed meadow.

5.3.8 Willow Garth (Ordnance Survey grid ref. TA 126676)

Willow Garth is a 5 ha wetland reserve managed by the Yorkshire Wildlife Trust on a five year lease. The reserve borders the Gypsey Race, a stream which carries water draining from the chalk catchment of the Great Wold Valley. Springs rise along a spring-line on the valley sides and there are at least five of these springs within the reserve, creating fen conditions in the heart of a chalkland landscape. The valley is periodically flooded by the spate waters of the Gypsey Race, although the frequency of this event has been reduced by water extraction and deep land drainage. Willow Garth was probably one of a series of such valley fens but now it is the last remaining piece of ancient carr woodland in the Great Wold Valley (Plate 4). The waterlogging of the soil allowed peat formation, and in 1984 this site was designated an S.S.S.I. for the value of its Quaternary record.

The main body of the reserve is a mixed deciduous woodland dominated by Populus alba and Alnus glutinosa in the wettest areas and Ulmus procera, Aesculus hippocastanum, Acer

PLATE 4 WILLOW GARTH, AN ANCIENT CARR WOODLAND LYING
IN THE GREAT WOLD VALLEY.

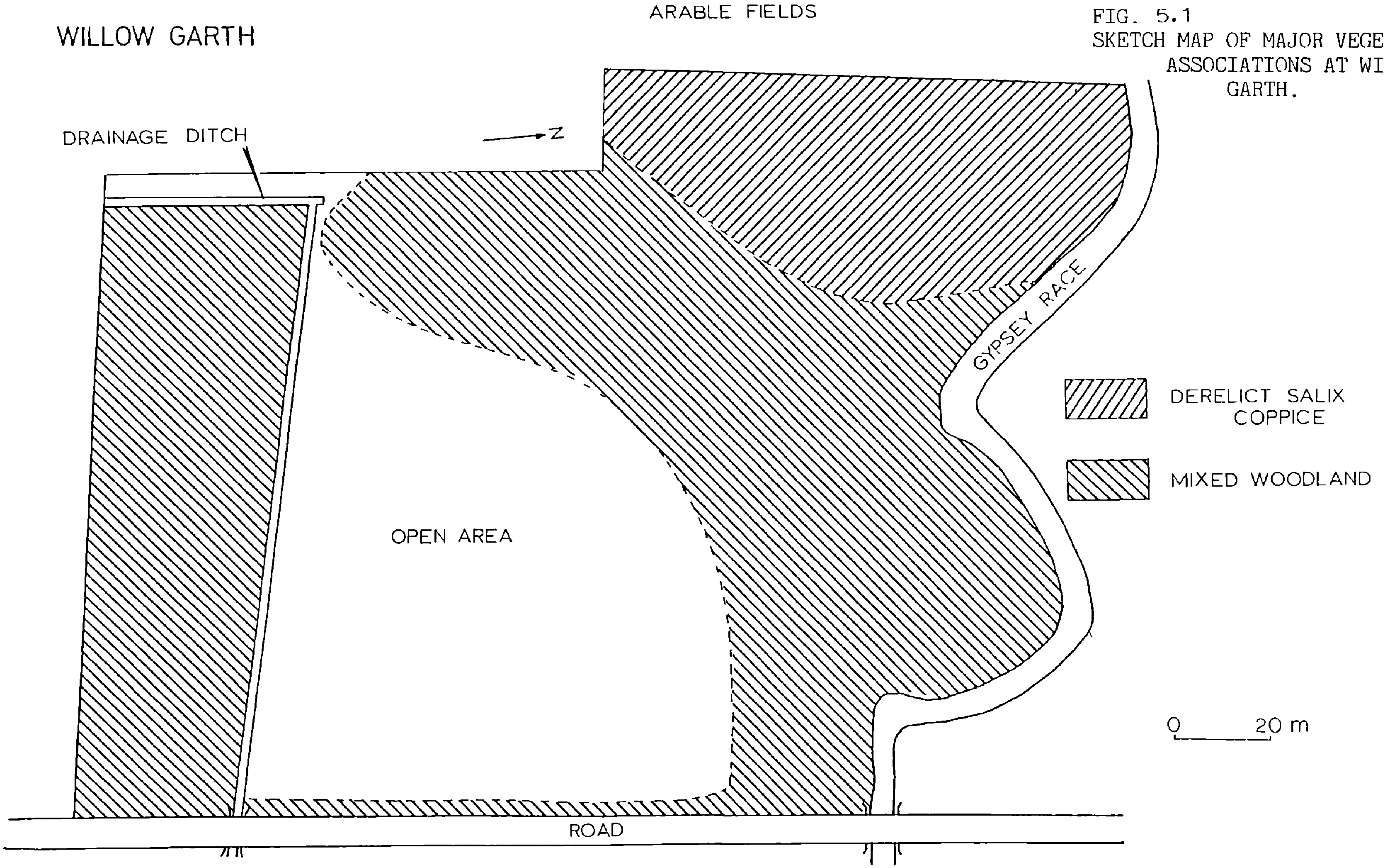


FIG. 5.1
SKETCH MAP OF MAJOR VEGETATION ASSOCIATIONS AT WILLOW GARTH.

pseudoplatanus and *Fagus sylvatica* in the drier areas. In the southern fringe of the reserve *Larix decidua* and *Pinus sylvestris* struggle to survive; these are a testament to an abandoned plan to turn the area into an arboretum during the early eighteenth century (Mr. G. Brown pers comm.). The western end of the reserve is a derelict osier (*Salix viminalis* and *S. purpurea*) bed which has not been managed for many years (Fig. 5.1).

Within the reserve there are two *Quercus robur* and a solitary *Betula pendula*. *Viburnum opulus* is locally abundant and *Acer campestre* is present in low numbers. The hedges bounding the reserve to the east and west are species rich containing: *Prunus spinosa*, *Crataegus monogyna*, *Salix capraea*, *Acer campestre* and *Sambucus nigra*.

The waterlogging of the soil has led to the trees forming wide plate-like root bases which are susceptible to wind-blow. The fallen trees (Plates 5 and 6) allow a vortex of wind to cause further forest destruction, with the result that an open area has formed in the middle of the reserve. This area, pitted with depressions where root bases have torn free of the earth, has become rank with tall herb species such as *Filipendula ulmaria*, *Epilobium hirsutum*, *Galium aparine*, *Urtica dioica* and *Angelica sylvestris* (Plate 7).

In the Gypsey Race *Sparganium* spp. and *Iris pseudacorus* are the commonest emergent species (Plates 8 and 9), but submerged aquatic plants are not apparent in this section of the river. A drainage ditch which runs through the reserve forms the southern margin of the open area and within it may be found *Caltha*

PLATE 5 THE PLATE-LIKE ROOT-BASE OF A FALLEN
POPULUS ALBA AT WILLOW GARTH.

PLATE 6 SALIX FRAGILIS DAMAGED BY WINDBLOW AT WILLOW GARTH.

PLATE 7 FILIPENDULA ULMARIA AND EPILOBIUM HIRSUTUM ARE THE DOMINANT GROUND FLORA IN THE UNSHADED PORTIONS OF WILLOW GARTH. 1M QUADRAT SHOWN FOR

PLATE 8 THE GYPSEY RACE AT WILLOW GARTH (AUGUST 1985).

PLATE 9 EMERGENT VEGETATION IN A SLOW MOVING SECTION
OF THE GYPSEY RACE AT WILLOW GARTH (AUGUST 1985)

palustris, Nasturtium microphyllum, Veronica beccabunga, Juncus articulatus, Iris pseudacorus and Sparganium spp.. Where drainage works disturbed the banks in 1982, Scrophularia aquatica, Listera cordata, Dactylorhiza fuchsii, Mentha aquatica and Myosotis sylvatica have colonised the bare ground. A similar assemblage of plants was noted from where the fallen tree in Plate 5 had disturbed the soil surface. Filipendula ulmaria and Epilobium hirsutum are invading these communities and it is to be expected that unless there is further disturbance they will be shaded out by these vigorously growing herbs. On the wettest portion of the reserve Iris pseudacorus, Angelica sylvestris and Urtica dioica were the herb dominants growing among the collapsed, but regenerating, trunks of Salix fragilis (Plate 10). The fallen tree at this point was observed to be female and so the proximity of that individual would not be reflected in the modern pollen spectrum although it might be seen in the propagule samples.

Moss polsters were collected from the fallen willow trunks and from two other locations in the woodlands surrounding the open portion of the site. Five pollen traps were set within the reserve, but four were vandalised. The fifth contained a stubbed-out cigarette but was otherwise undamaged. This latter trap was located within the Iris pseudacorus and Angelica sylvestris community, in the wettest portion of the fen, two metres away from where the samples for palaeoecological analysis were extracted.

PLATE 10 <u>IRIS PSEUDACORUS</u> IS THE DOMINANT HERB IN THE WETTEST PORTIONS OF WILLOW GARTH.

5.3.9 Littlewood (Ordnance Survey grid ref. SE 955374)

The Littlewood is an 11.5 ha ancient woodland near North Newbald on the ridge of the Yorkshire Wolds. The woodland has been worked as a coppice in the past and can be divided into three broad types of woodland. The western part of the wood is dominated by mature specimens of *Quercus robur*, *Acer pseudoplatanus*, *Betula pendula*, *Corylus avellana* and *Fraxinus excelsior*. Less frequent members of this association are *Acer campestre* and *Malus* sp.. The ground flora contains *Dryopteris filix-mas*, *D. carthusiana*, *Hyacinthoides non-scripta*, *Allium ursinum* and *Oxalis acetosella*.

The second of the vegetation associations at Littlewood is a parkland area which was created by the selective thinning of the forest already described. The shrub layer is much reduced and only specimen trees of *Quercus robur* and *Betula pendula* were retained. A dense cover of *H. non-scripta* in the spring gives way to *Dryopteris filix-mas* in early summer.

In the third association there is a dense growth of the secondary forest taxa, *Acer pseudoplatanus* and *Fraxinus excelsior*. It is unclear as to whether this is a planted stand or a naturally regenerating stand growing on a site which was clear-felled during the early 1940's. There are few mature trees in this association although the ground flora is one of an ancient woodland with such species as *Allium ursinum*, *H. non-scripta*, *Dryopteris filix-mas*, *D. carthusiana*, *Melica uniflora*, *Oxalis acetosella* and *Anemone nemorosa*.

Four traps were set within this wood, two in the least disturbed area and one in each of the other two associations. All were recovered intact.

5.3.10 Anston Stones Wood (Ordnance Survey grid ref. SK 531831)

This 33.7 ha woodland clads the sides of a deep north-south valley on the Magnesian Limestone near Maltby, South Yorkshire. The dominant trees throughout much of the wood are *Tilia cordata*, *T. platyphyllos*, *Quercus petraea*, *Q. robur*, *Fraxinus excelsior* and *Ulmus glabra*. Anston Stones Wood was specifically mentioned by Pigott (1969) as being one of the woodlands in which it is likely that the two species of *Tilia* occur together naturally. This was taken to imply considerable antiquity and that the woodland was probably a remnant of the ancient *Tilia* forest of South Yorkshire and Derbyshire (Pigott, 1969; Merton, 1970).

Within Anston Stones Wood Dutch-Elm disease has affected many of the *U. glabra* rendering them moribund. On the western slope of the valley is a hangar of *Fagus sylvatica* which is of a totally different character from the rest of the woodland. Here there is little or no understorey and the ground flora is sparse, largely composed of *Rubus fruticosus*, *Mercurialis perennis* and *Hedera helix*. This contrasts markedly with the abandoned hazel coppice under the canopy trees in the rest of the wood. The hazel stools are large, although clearly not worked for a considerable time. The ground flora in this section of the wood includes: *Galium odoratum*, *Neottia nidus-avis*, *Melica uniflora*, *M. nutans*, *Daphne laureola*, *Hyacinthoides non-scripta* and *Oxalis acetosella*. All of these are suggested by Peterken (1981) to have strong affinities for ancient woodlands. Where there are bare limestone crags *Oxalis acetosella*, *Moehringia trinervia* and *Phyllitis scolopendrium* grow.

A third woodland type is present on flat ground above the eastern valley slope. Here a dense *Betula pendula* and *Quercus petraea* woodland grows. Mature specimens of both species are present, plus many regenerating *B. pendula*. The ground flora is dominated by a member of the Labiatae, possibly*Lamiastrum galeobdolon*, but it was not found in flower and so identification was uncertain. Dense clumps of *Rubus fruticosus* grow where there is little shade.

Of the five pollen traps set in this wood, one was set in the *Quercus*-*Betula* woodland, one on the edge of the *Fagus sylvatica* dominated area and the remainder in the *Tilia*-*Corylus* woodland. All were recovered, but one of them had been broken into and the acetate yarn partially removed, this may have been rodent damage.

5.3.11 Kingswood (Ordnance Survey grid ref. SK 542899)

The Kingswood is a 52.8 ha woodland near Maltby, South Yorkshire. It is regarded by the Nature Conservancy Council as the most important woodland for nature conservation on the Southern part of the Magnesian Limestone in Great Britain. Dominated by *Tilia cordata* and *Taxus baccata* this woodland is characteristic of those described by Pigott (1969) as remnants of the ancient lime woodlands of Britain. Laughton Pond, an artificial lake which was probably created during monastic times has been created by damming the stream which flows in the valley bottom. The margin of the pool would appear to vary slightly, creating a narrow flushed margin which contains characteristic fenland plants such as Carex spp., Nasturtium aquaticum and Caltha palustris. Alnus glutinosa and Salix spp. were also present along the lake margin, the latter forming a carr woodland near the inlet of the pool.

On the valley slopes above the pool there is a rich deciduous woodland in which Tilia cordata, Taxus baccata, Quercus spp., Ulmus procera, Betula pendula and Corylus avellana are common. Fagus sylvatica also occurred in local stands. The ground flora was generally dominated by Mercurialis perennis and in slightly less shaded locations by Pteridium aquilinum and Rubus fruticosus. Gramineae are sparse in the wood with scattered occurrences of Melica uniflora and an occasional clump of Festuca spp., Dactylis glomerata and Hordelymus europaeus. Other herb species include Convallaria majalis, Lathraea squamaria and Helleborus viridis.

Where rides had been created it was apparent that wind-blow was affecting some trees, particularly large Taxus baccata. Several specimens were observed to have fallen, exposing a wide shallow root base which had failed to support the tree in the shallow soils overlying the limestone. Growing in the openings created by the fallen trees were: Lamiastrum galeobdolon, Primula spp. and Prunella vulgaris. Evidence that the woodland had once been coppiced was apparent particularly on the Corylus avellana stools although there were also some multiple-stemmed Tilia cordata suggesting that these too may have once been coppiced.

Five pollen traps were set, four amongst the Tilia woodland

and one on the margin of the lake. All were recovered intact.

5.3.12 Leven Canal (Ordnance Survey grid ref. TA 105449)

The 5 km long Leven Canal, situated about 3 km north of Pulfin Bog, was constructed in 1802 to connect Leven to the River Hull. The canal was cut off from the river in 1934 and has been an S.S.S.I. since 1962. Boat traffic is prohibited at the Leven end of the canal, and a rich aquatic flora has become established. Crackles (1968) suggested that this community may owe much of its diversity to a relict late-glacial flora which existed in the Leven Carrs when the canal was built. The Carrs have since been drained but the flora is retained in the canal. Crackles based her argument on the occurrence of disjunct species such as: Schoenoplectus lacustris, Calamagrostis canescens and C. stricta (Crackles, 1977).

At the Leven end of the canal the banks are lined with Phragmites australis, Carex rostrata and Filipendula ulmaria. Specimens of Alnus glutinosa overhang the canal at some locations, but the water is generally unshaded. The obligate aquatic flora includes: Potamogeton lutens and P. natans, Sagittaria sagittifolia, Alisma plantago-aquatica and Nuphar lutea. This site was used to collect surface sediment samples for seed, bryophyte and mollusc analogue studies.

5.3.13 Brandesburton Gravel Pit (Ordnance Survey grid ref. TA 098477)

Slightly to the north-west of Brandesburton lies a string of gravel pits some of which are still actively worked and some of which are abandoned. The gravel extraction has been going on for many years on what was the eastern limit of the now drained Leven Carr. Some of the abandoned pits offer an extremely eutrophic environment and plant colonisation is rapid. The result is a diverse aquatic and emergent flora.

A small gravel pit *c.* 20 m x 50 m with no inflow or outflow stream was located. The pool supported a rich growth of aquatic macrophytes amongst which the dominant taxa were: *Typha* sp., *Potamogeton* sp. and *Alisma plantago-aquatica*.

The landscape round about was treeless, and heavily disturbed by the quarrying activities. The gravelly clay hummocks between the ponds were not completely vegetated but supported a flora of invasive weed species such as *Urtica dioica*, *Chamaenerium angustifolium* and *Rumex* spp..

A sample of the pond mud was collected from between the *Typha* sp. stand and the *A. plantago-aquatica* growth in the deeper water of the pond. This sample was used to provide modern analogue data for 'macrofossil' remains from a small, enclosed pool habitat.

5.4 VEGETATION ANALYSIS

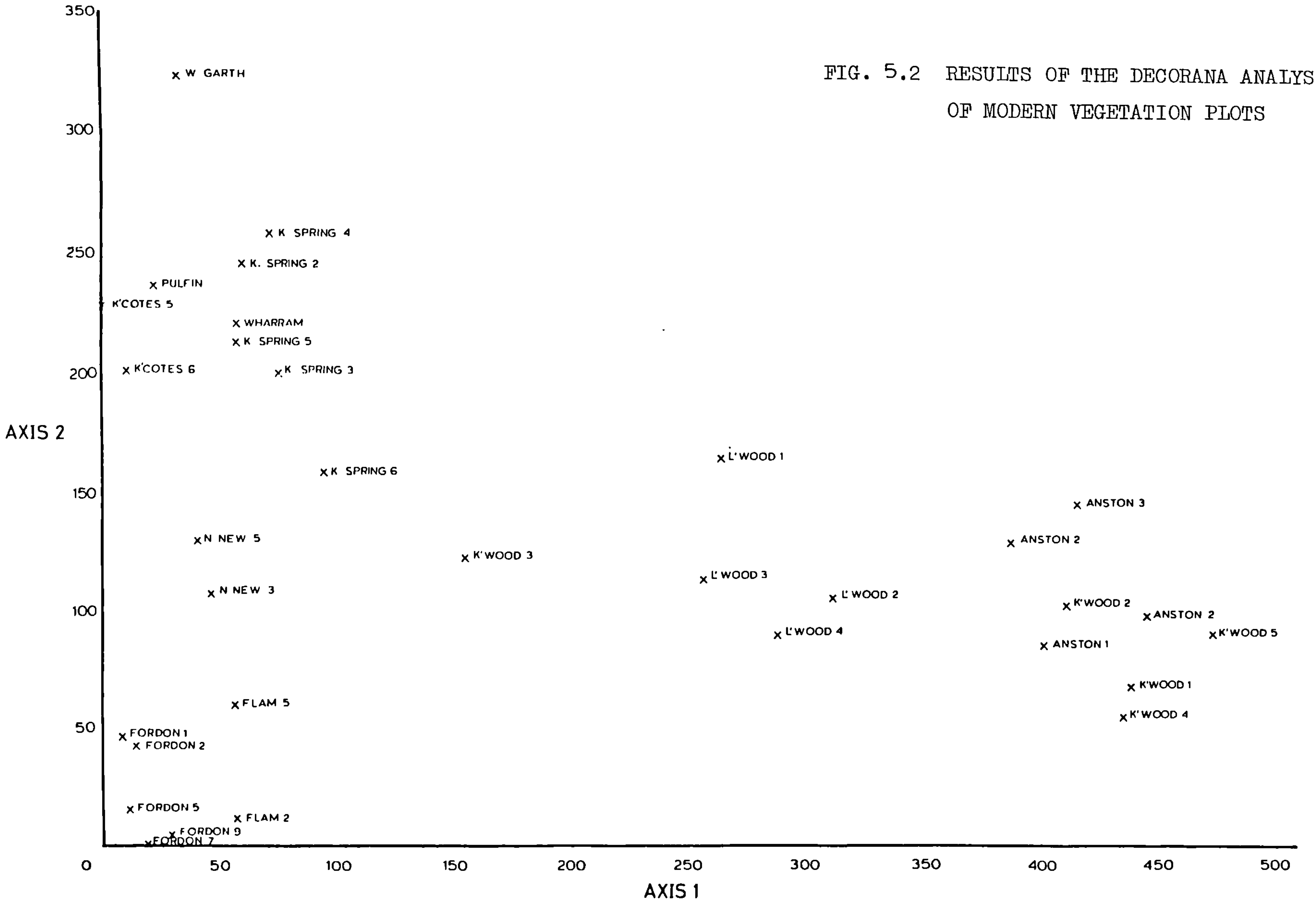
5.4.1 Classification of Modern Vegetation Survey Data

Vegetation patterns, even when modified by man, often form a continuum of variation from one community to the next. Man, when analysing nature, attempts to divide this variation into discrete units, a practice which Goodall (1954) argued against. In statistical terms continuous variation is best measured by an ordination technique whilst a classificatory technique will impose a structure of units upon nature. Our grasp of clines and gradients, however, is not as good as it is of discrete groups, and it is much easier to discuss neatly, even if somewhat artificially, defined groups. For this reason classification generally renders more interpretable results than ordination. Gauch and Whittaker (1981) recommend that the two statistical techniques should be used together and this is the practice followed in this study. For the convenience of discussion the TWINSPAN groupings of the herb survey data are being taken as the classificatory units, although it must be borne in mind that a computer program cannot detect quirks in a data set which are obvious to the human analyst.

5.4.2 The Herb Flora

As can be seen from the DECORANA analysis (Fig. 5.2) of the herb flora data set, an environmental gradient (axis 1) was indicated from the grasslands of Fordon Chalk Bank and Kiplingcotes Quarry to the woodlands of Kingswood and Anston Stones Wood. The second axis suggested the presence of an environmental gradient between Fordon Chalk Bank and Willow

FIG. 5.2 RESULTS OF THE DECORANA ANALYSIS OF MODERN VEGETATION PLOTS



Garth.

It is the nature of ordination techniques that the first axis will explain most of the variance and thereafter the axes will explain less and less of the information in the data set. An indication of the strength of each axis, the amount of the residual variation which it accounted for, could be deduced from the eigenvalue for that axis. In DECORANA where the eigenvalues do not total 1 they must be treated as indications of strength relative to each other.

In this data set the eigenvalues were:

axis 1	0.778
axis 2	0.417
axis 3	0.277
axis 4	0.152

This suggests that axis 1 has explained almost twice as much of the variance as axis 2 and over three times as much as axis 3. In general the first two axes should be readily interpretable, but axes three and four can sometimes be rather obscure in their meaning. Such was the case in this analysis: the third and fourth axes were not readily interpretable and so have been left aside.

Axis 1 of the herb data probably represented a gradient of decreasing light availability in the herb layer. The ordination of species placed *Ononis repens*, *Silene* spp. and *Centaurea scabiosa* at the negative extreme and *Pteridium aquilinum*, *Arctium pubens* and *Ligustrum vulgare* at the positive extreme of this axis (Fig. 5.3).

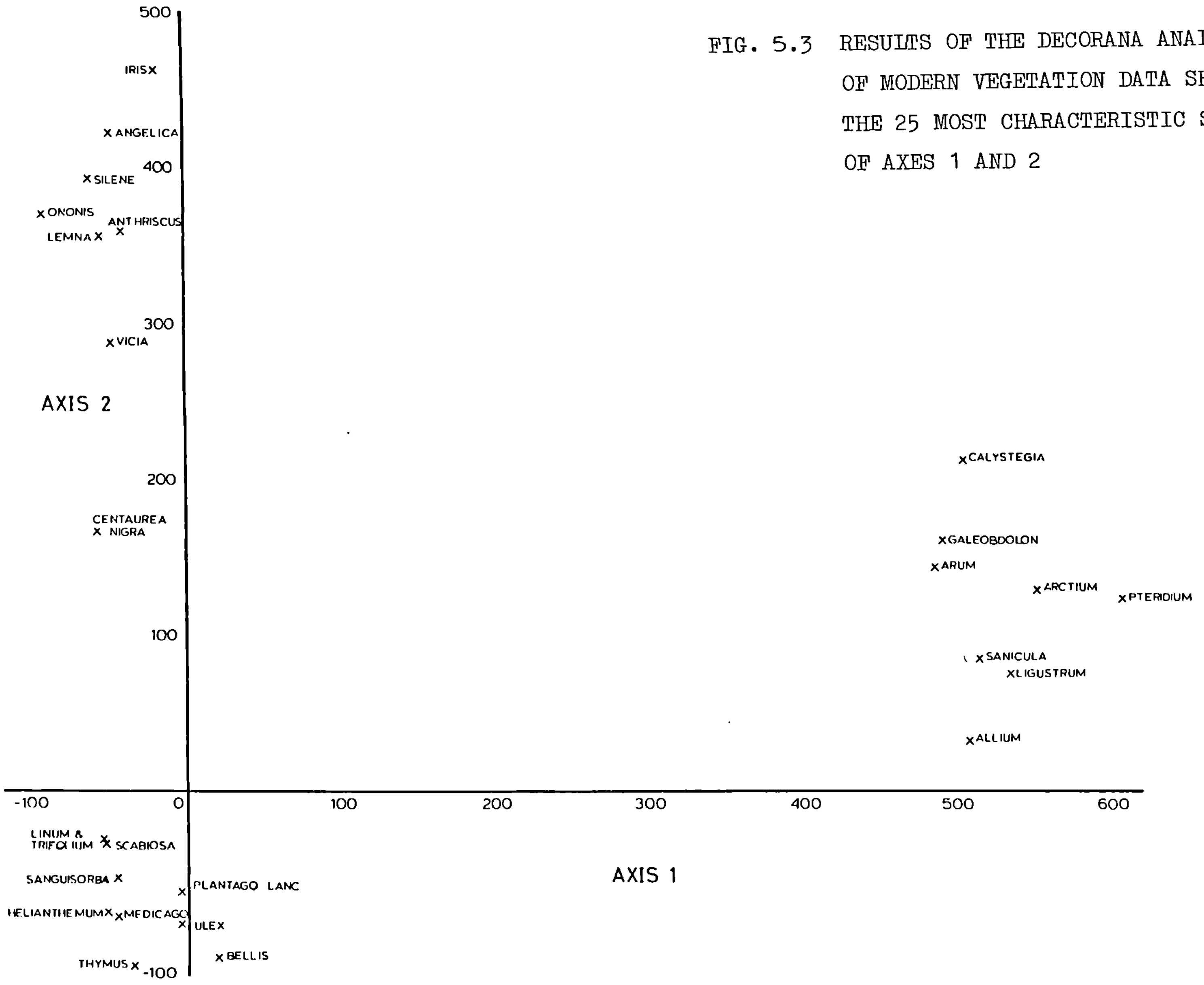


FIG. 5.3 RESULTS OF THE DECORANA ANALYSIS OF MODERN VEGETATION DATA SHOWING THE 25 MOST CHARACTERISTIC SPECIES OF AXES 1 AND 2

Axis 2 was characterised by Thymus praecox, Bellis perennis and Ulex europaeus at the negative extreme and Silene spp., Angelica sylvestris and Iris pseudacorus at the positive extreme. This suggested an environmental gradient of increasing soil moisture, but the wetland sites of Pulfin Bog and North Newbald were not grouped at the positive extreme of the axis. Alternatively this may have been an axis reflecting soil nutrient status. At the negative extreme were the chalk grassland sites which may have been deficient in phosphates and nitrates. In contrast the seasonal flooding which takes place at Willow Garth has produced a rich organic silt which, judging from the abundance of Silene dioica and Urtica dioica, is rich in phosphates and nitrates. Another possible gradient represented by this axis was one of decreasing drought stress. Plants growing on the thin permeable soils of the northern chalklands were subject to 90 to 109 mm of water deficit during the summer months (Smith, 1980). The thicker alluvial soils, moistened by springs and shaded by trees, at Willow Garth would not have offered such an arid environment. The shading of the site may have been important in this respect so that even at times of low spring seepage the site did not dry out. The fen at North Newbald which had no shading trees may have been more susceptible to drought stress than Willow Garth and hence was not positioned so far along this environmental gradient.

The classification analysis (Fig. 5.4) separated the ancient woodlands of Anston Stones Wood, Littlewood and Kingswood from all the other sites at the first divisive level. This division was characterised by the negative group (0) containing

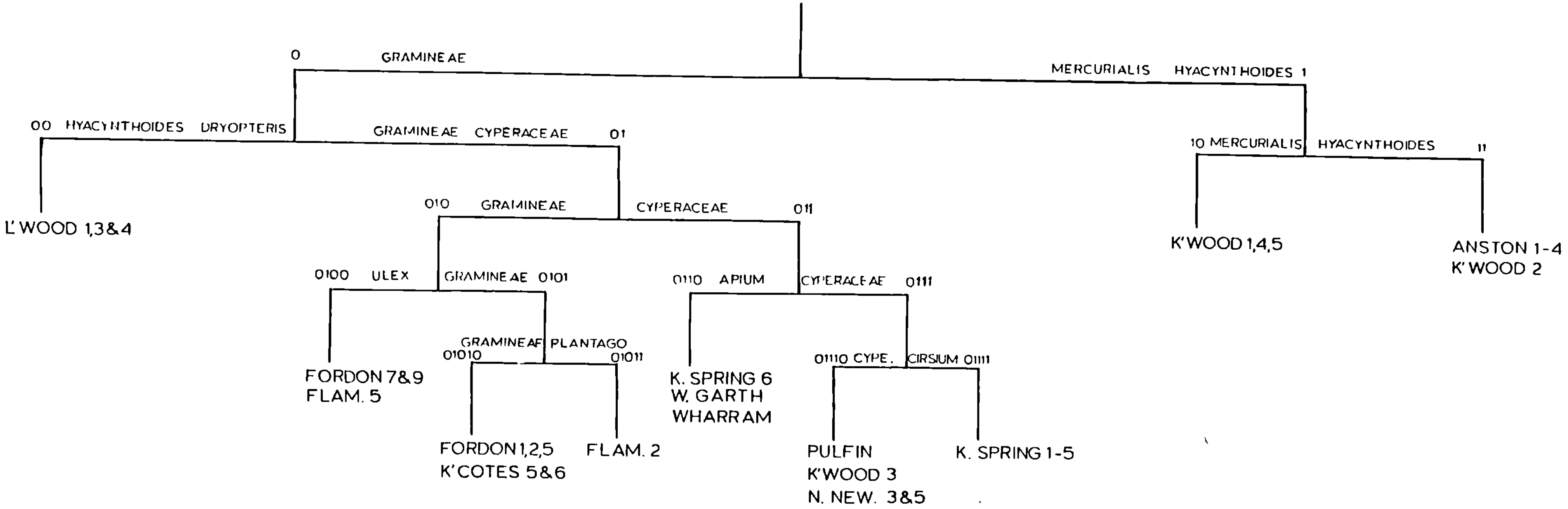


FIG. 5.4 RESULTS OF THE TWINSPAN ANALYSIS OF THE MODERN VEGETATION SURVEY

relatively high values of Gramineae and the positive group (1) containing Mercurialis perennis, Hyacinthoides non-scripta and Rubus fruticosus agg.

That three of the plots from Littlewood were not placed with the other ancient woodlands was probably a reflection of the degree of recent disturbance in Littlewood, e.g. selective felling and coppicing, compared with the less managed plots recorded in Littlewood 2 and the woodlands of the Magnesian Limestone.

The second divisive level split Littlewood 1, 3 and 4 into the negative group (00), characterised by H. non-scripta, Dryopteris and Epilobium. In the positive group (01) were placed the grasslands and wetlands as indicated by the presence of high values of Gramineae and Cyperaceae. The wetland sites include Kingswood 3, for although this herb community was shaded, the location on the lake margin gave this sample the character of a wetland group. Similarly Willow Garth occurred in this group and not amongst the woodland communities.

At the second divisive level the woodland group was sudivided into those plots rich in Mercurialis perennis and Rubus fruticosus agg., e.g. Kingswood 1, 4 and 5, and those plots rich in Hyacinthoides non-scripta, Epilobium spp. and Labiatae spp., e.g. Anston 1 - 4 and Kingswood 2. This represented a division between the heavily shaded and the more lightly shaded woodlands.

The third divisive level resulted in the separation of grasslands into the negative group (010) and wetlands into the positive group (011). This division was based on the abundance of Gramineae, *Ulex europaeus* and *Sanguisorba minor* in the grassland assemblages and *Juncus* spp., Cyperaceae, *Filipendula* spp. and *Galium* spp. in the wetland associations.

The ecological value of the separation of Littlewood 2 from the Anston Stones Wood plots is questionable, and so this division was not utilised further.

The fourth divisive level separated the grassland groups into a negative group (0100) consisting of plots dominated by *Ulex europaeus*, and a positive group (0101) of Gramineae-dominated grasslands. The wetlands were subdivided into those dominated by Cyperaceae in a positive group (0111) and those dominated by *Apium nodiflorum*, *Urtica dioica* and *Galium* spp., in the negative group (0110). The negative group contained the seasonally flushed, nutrient rich sites of Kiplingcotes Spring 6, Wharram Percy and Willow Garth. The fifth divisive level resulted in the formation of a negative group (01010) of grasslands containing the chalk grasslands of Fordon Chalk Bank and Kiplingcotes, and a positive group (01011) characterised by the presence of *Plantago lanceolata* and *Primula vulgaris* on the sea cliff plot of Flamborough 2.

The wetlands subdivided into the rich fenland sites of Pulfin Bog, Kingswood 3 and North Newbald in the negative group (01110) in which Cyperaceae was the characterising taxon, and a positive group (01111) of the seasonally wet locations, e.g. Kiplingcotes Spring plots 1 - 5, which were characterised by *Cirsium* spp. and *Epilobium* spp..

5.4.3 Arboreal Data Classification

The TWINSPAN analysis of the woodland canopy area data resulted in three basic woodland types being separated. The first divisive level grouped those sites containing Alnus glutinosa, with the result that Kingswood 3 and Willow Garth were placed into the positive group (1). All the other sites were placed into the negative group (0).

The second divisive level separated the sites in group 0 into a positive group (01) of sites rich in Quercus spp. and Corylus avellana from a negative group (00) of sites dominated by Tilia and Taxus baccata. The Littlewood plots formed the negative group, whilst those of Anston Stones Wood and Kingswood were allocated to the positive group.

These groups corresponded broadly to the Alnus glutinoseae (Braun-Blanquet and Tuxen 1943), the Quercetea Robori-Petraeae (Braun-Blanquet and Tuxen 1943) and the Querco-Fagetea (Br-Bl et Vlieg 1937), alliance Tilio-Acerion (Klika 1955).

Until the Nature Consrvancy Council produce the National Vegetation Classification the British woodlands will probably remain as oddities which frequently do not fit the European system of nomenclature. In the absence of a satisfactory European style of nomenclature, the woodland classification system proposed by Peterken (1981) was utilised in this study as it was specifically designed for British woodlands.

If the classification derived from the TWINSPAN analysis of woodlands and that of the ground flora are used together, a list of the communities recorded can be established (Table 5.1).

Vegetation type	Characterising spp.	Locations
Wet valley Alder wood	*Alnus glutinosa*., *Salix*, spp. *Urtica dioica*., *Galium* spp. Cyperaceae	Willow Garth Kingswood 3
Willow wood	*Salix* spp., *Myosotis* sp., *Urtica dioica*, *Apium nodiflorum*	Kiplingcotes Spring 6
Lowland Hazel-Oak wood	*Quercus* spp., *Corylus avellana*, Gramineae, *Hyacinthoides non-scripta* *Dryopteris filix-mas*	Littlewood 1 - 4
Oak-Lime-Ash wood (a)	*Tilia cordata*, *Taxus baccata*, *Rubus fruticosus*, *Mercurialis perennis*	Kingswood 1, 4, 5
(b)	*Tilia cordata*, *Quercus* spp., Ulmus spp., Labiatae *Hyacinthoides non-scripta* *Epilobium* spp.	Anston 1, 2, 4.
(c)	*Tilia cordata*, *Fagus sylvatica*, *Hyacinthoides non-scripta*	Kingswood 2, Anston 3

Labiatae

Vegetation type	Characterising spp.	Locations
Rich fen meadow	Gramineae, Cyperaceae, *Juncus* spp., *Filipendula. ulmaria*	North Newbald 3, 5, Pulfin Bog
Nutrient enriched fen meadow	Gramineae, *Urtica dioica*, *Apium nodiflorum*	Wharram Percy
Seasonally flushed grassland	Gramineae, *Cirsium* spp., *Epilobium* spp., *Rumex* spp.	Kiplingcotes Spring 1 - 5
Grazed chalk grassland	Gramineae, *Thymus praecox*, *Sanguisorba minor*	Fordon 1, 5, 8. Kiplingcotes 5, 6, Flamborough 2
Scrubby chalk grassland	*Ulex europaeus*, Gramineae	Fordon 7, 9 Flamborough 5.

Table 5.1. Semi-natural plant communities on calcareous substrata in the vicinity of the Yorkshire Wolds.

5.5 REPRESENTATION OF TAXA

The pollen yield from the pollen traps is shown in Fig. 5.5 where it is expressed as a percentage of the dry land pollen sum. Fig. 5.6 shows the percentage weighted canopy area for arboreal taxa in woodland sites, and the percentage abundance of the herb cover as estimated from the line transects. Plotted with these are the weighted arboreal pollen percentages as derived from the R-rel values calculated in chapter 5. These are only provided for the woodland sites otherwise the underlying criteria for the R-rel model are not being met. For the non-woodland sites the arboreal pollen is shown as presence or absence (Fig. 5.6). The pollen record shown for the non-arboreal flora is the percentage of total non-arboreal pollen and spores. The sequence in which the sites were ordered in the diagram was drawn from axis 1 of the herb vegetation DECORANA analysis, modified by moving Willow Garth one place so as to be next to Kingswood 3. This was to facilitate the use of the TWINSPAN zonation in labelling the diagram.

Janssen (1973) stated that the local pollen deposition would vary widely according to local fluctuations in species abundance and the poor dispersal of herbaceous pollen taxa. Birks (1973) used the term 'local' to describe pollen taxa morphologically indistinguishable from those growing within, or close to, the quadrat area. Janssen (1973) defined the local pollen component as having many pollen types, the values of which were high but often irregular, facilitating the recognition of minor vegetation types.

The data obtained from the vegetation survey and those from the pollen analysis were compared to obtain estimates of representation. Firstly, by comparing the data for pollen and vegetation from a site it was possible to determine how many of the vegetation taxa were represented in the pollen record. The inverse of this was to establish how many taxa recorded in the pollen spectrum were not recorded in the quadrat. This helped to establish the proportion of adjacent and local representation that is present in the sample. It also provided an estimate as to the accuracy of a vegetation reconstruction based on pollen data. In order to estimate the completeness of the pollen representation of the adjacent flora the percentage presence of each of the taxa common to the quadrat and the pollen record were summed. This established a crude figure for the percentage of the vegetation cover which had some representation in the pollen record. However, it did not confirm that the pollen was derived from individuals of that taxon lying within the quadrat area.

Summing the percentages for the pollen taxa which may have originated from within the quadrat yielded a maximum value for the adjacently derived pollen. The remainder could be divided into those taxa likely to be present in that vegetation type but which were not recorded in the survey and those which came from a different habitat (Fig. 5.5). These were the local and non-local pollen percentages as used by Birks (1973), Andersen (1973) and Bradshaw (1981a).

The pollen influx (grains cm^2 y^{-1}) was calculated from the pollen caught in the traps. This revealed a range of 790 to 18,147 grains cm^2 y^{-1}. In general the more sheltered the location for the trap the higher the pollen yield. Woodland locations and the deep hollow at Kiplingcotes Spring produced the highest counts whilst the open downland locations of Fordon and Kiplingcotes Quarry produced low yields.

Although it is possible that the traps were set too high to collect the full pollen yield from the grazed chalk grassland species it is more likely that this was a reflection of the higher pollen production of woodlands than grasslands. M.B.Davis _et al_. (1973) recorded a range of 14200 to 78300 grains cm^2 y^{-1} from deciduous forest with a mean value of 37300. R.B.Davis _et al_. (1975), also working in forests, obtained lower values, 1980 to 50160 grains cm^2 y^{-1} with a mean of 8760. This compared with a range of 790 to 14500 grains cm^2 y^{-1} obtained in this study.

From prairie habitats M.B.Davis _et al_. (1973) recorded 1000 to 15000 grains cm^2 y^{-1} with a mean of 9500 which represented a similar range to the 1000 to 18100 grains cm^2 y^{-1} obtained from non-woodland sites in this study.

Forests containing many anemophilous species would have been expected to produce and deposit more pollen than grasslands where many of the species present were entomophilous. This difference might be exacerbated by grazing pressure in grassland areas such as Fordon Chalk Bank. In these areas both pollen and seed production might be expected to be lower than in the ungrazed areas such as Kiplingcotes Spring.

5.6 MODERN ANALOGUE DATA FROM GRASSLANDS AND FENS

5.6.1 Naturally Disturbed Grasslands

The plot at Flamborough 2 was subject to soil slippage: this was evident from patches of soil where the turf sward had slumped forward. Another trap similarly located in the next small embayment was lost due to cliff erosion. On a steep incline between the clifftop and a sheer drop into the sea, there was a short turf sward. The presence of grazing rabbits was evidenced by a considerable concentration of rabbit dung. The grasses were dominated by fescues and Carex panicea was the commonest member of the Cyperaceae. Primula vulgaris, Cochlearia officinalis and Bellis perennis were colonising the bare ground. Centaurea nigra was also abundant (Fig. 5.6).

The pollen influx to this site was 3488 grains cm^2 y^{-1} and 91% of these could have been derived from species growing within 5 m of the sample point. The pollen sum included 7 arboreal taxa which must have been part of the long distance or regional pollen sum, as no trees were seen to grow within 2 km of the site. The herb taxa were identified to the same degree of determination as was possible amongst the fossil pollen taxa. This gave 11 herb taxa present in the modern vegetation within 5 m of the sampling point. Of these, 6 were represented in the pollen count, and a further 6 herb taxa from outside of the quadrat were also represented (Fig. 5.7). 95.3% of the pollen sum were found to be contributed by pollen taxa which would be likely to have representatives growing in that habitat and therefore constituted the maximum local pollen sum. Of the 4.7%, which were

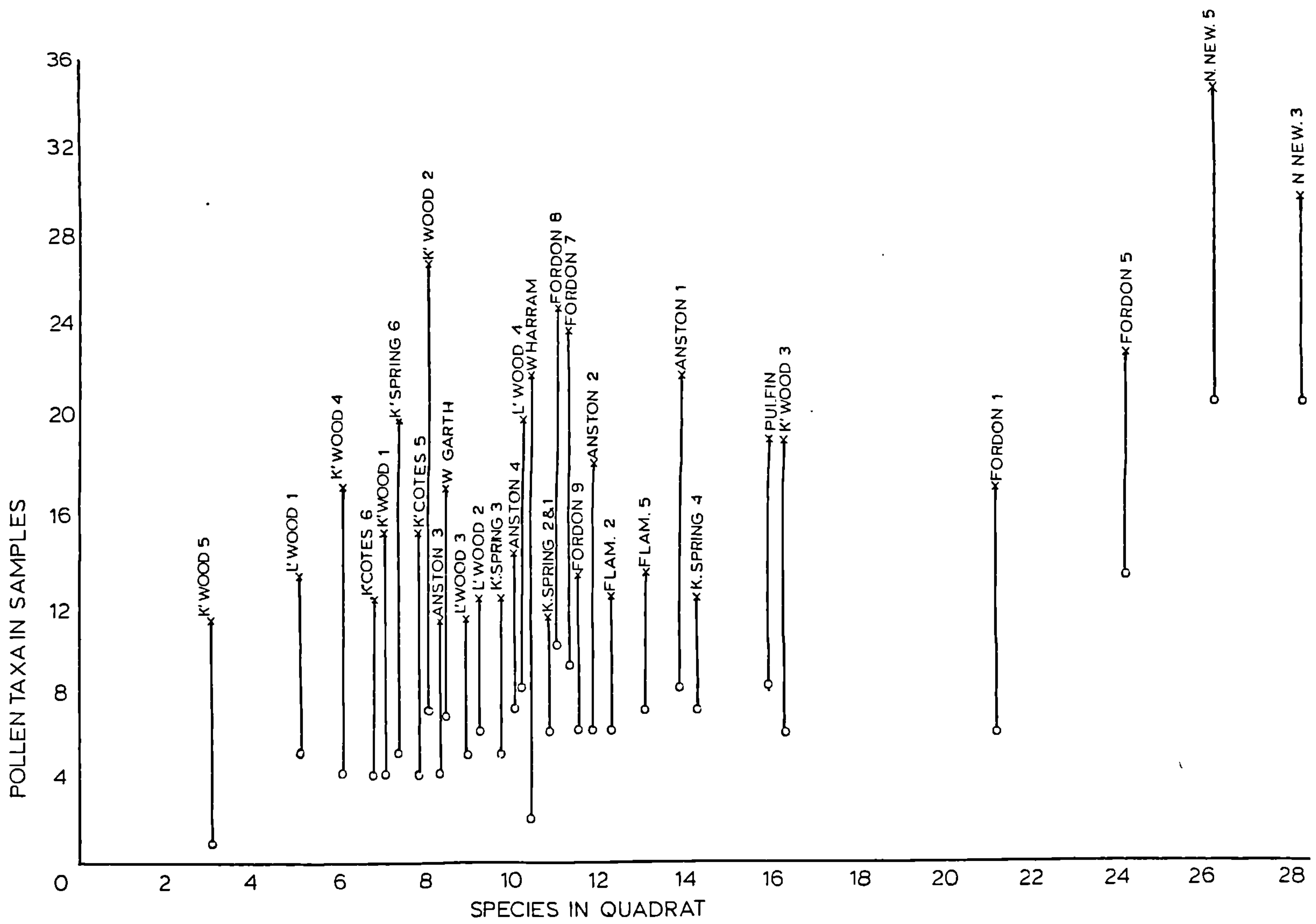


FIG. 5.7: NUMBERS OF POLLEN TAXA RECORDED AGAINST NOS. OF VEGTN. TAXA WITHIN 5 M OF SAMPLING POINT. o = number of pollen taxa known to be represented in the plot. x = total number of pollen taxa recorded from trap.

judged to be non-local pollen, 4.5% were arboreal pollen and the remainder were Cerealia pollen.

The pollen representation of this site was dominated by a 65.2% occurrence of Centaurea nigra. C. nigra was an extremely abundant plant along the cliff tops and in late August it can be seen to dominate whole embayments where the grassland is not cut. As this vegetation suvey was carried out in early July it is possible that C. nigra was under-recorded compared with its presence at the time of flowering. It is also possible that C. nigra was growing directly above the sampling point and was dropping anthers into the trap. The third possibility is that C. nigra was correctly estimated in the vegetation survey and that it was an over producer of pollen.

Of the five vegetation taxa at the site which went unrecorded in the pollen analysis, three were recorded from the seeds and fruits collected in the surface soil sample from this site. As some fruit taxa are identifiable to a more specific level there were 13 vegetation taxa present which it would be possible to distinguish in a seed record (Fig. 5.8). 8 of these were represented in the propagule record (Fig. 5.9). C. nigra accounted for 45% of the total, suggesting a local dominance of this taxon. Gramineae caryopses represented 8% of the total assemblage, whereas the pollen of this family had accounted for 16.9% of the dry land pollen sum. The vegetation survey recorded 68% of the contacts as being of Gramineae. Such a low representation amongst the fruits and pollen may be the result of preferential rabbit grazing in which the flower stalks of Gramineae were eaten off whereas those of Centaure nigra were

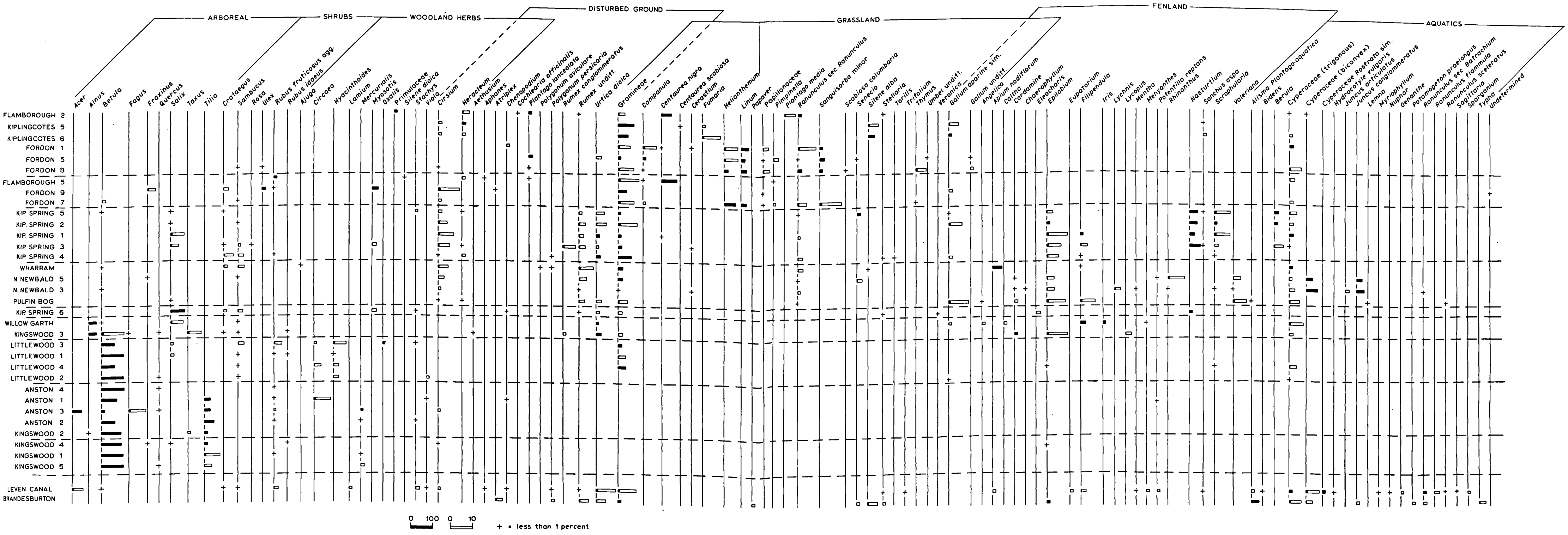


FIG. 5.8 PLANT PROPAGULES FROM MODERN ANALOGUE SITES

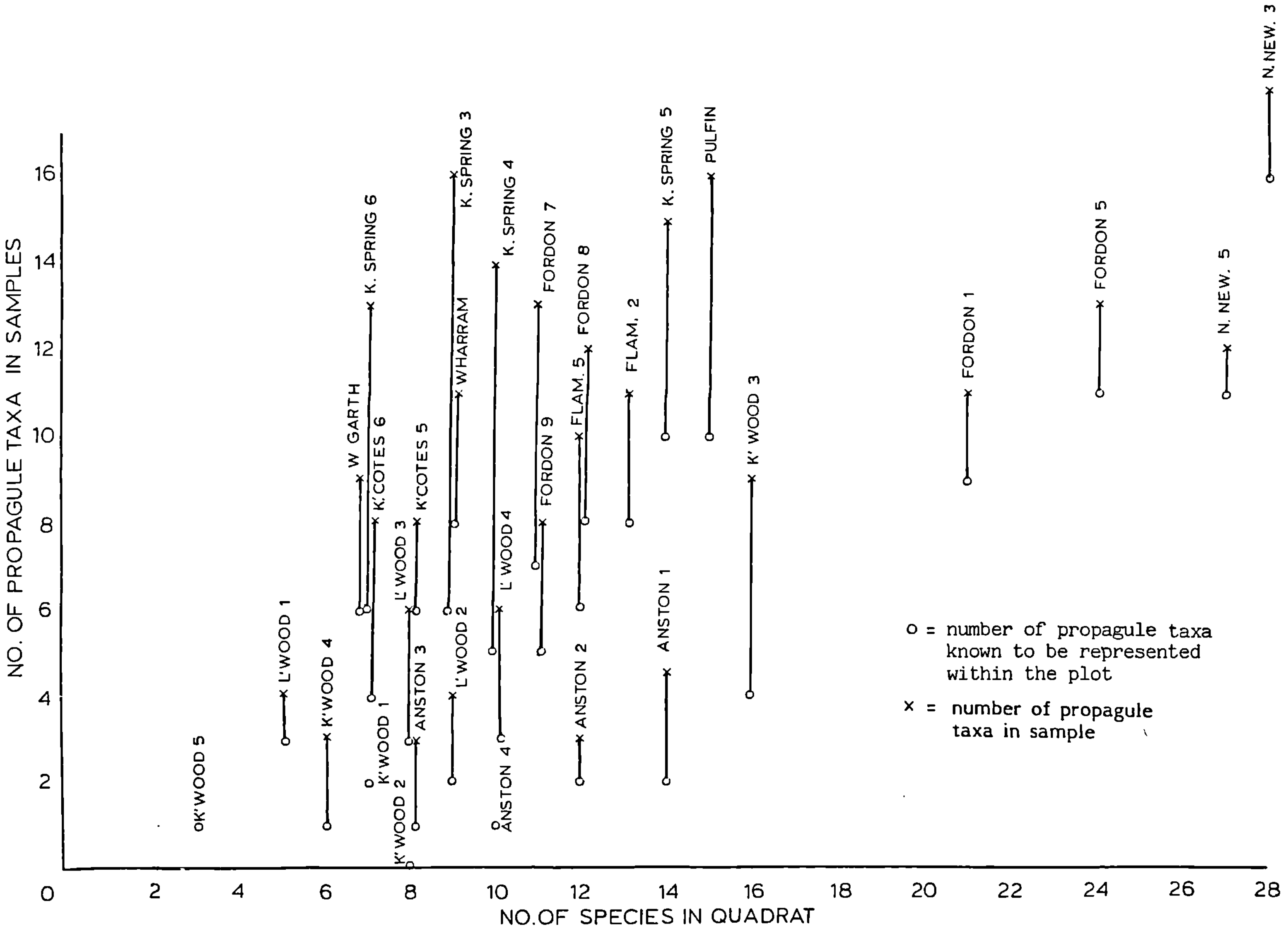


FIG.5.9: NUMBERS OF PROPAGULE TAXA RECORDED AGAINST NOS. OF TAXA WITHIN 5 M OF SAMPLING POINT AT MODERN ANALOGUE SITES.

left.

The two taxa present in the vegetation survey, but absent from either the pollen or propagule records, were Lotus (4%) and Orchidaceae (<1%), thus 95% of the herb flora had some representation. No pteridophytes were recorded at this quadrat; the bryophytes included Lophocolea bidentata and Eurynchium cf. praelongum.

The mollusc fauna, extracted from the same soil sample as the plant propagules, contained 8 species, of which most were catholic in their habitat range. The concentration of testae was 193 per litre of soil. Lauria cylindracea, which shows a preference for dry areas, attained a value of 34%; this was the only sample in which this species was found. Punctum pygmaeum (3%) a mollusc which is often associated with dry grassland, but which will also live in marshes, was also present (Fig. 5.10). The presence of Aegopinella nitidula and Vitrea crystallina which, although catholic in their choice of habitat, are usually associated with a moist or shaded environment, suggested that the cliff top microclimate of this north facing site was cool and moist.

5.6.2 Coarse Grassland

The two grassland sites at Kiplingcotes Quarry were of forb-poor chalk grassland. Brachypodium pinnatum dominated this grassland, growing to a height of 0.6 to 0.8 m, shading out all but the most resistant herbaceous species. In autumn the leaves of B. pinnatum, which are unpalatable to sheep and rabbits,

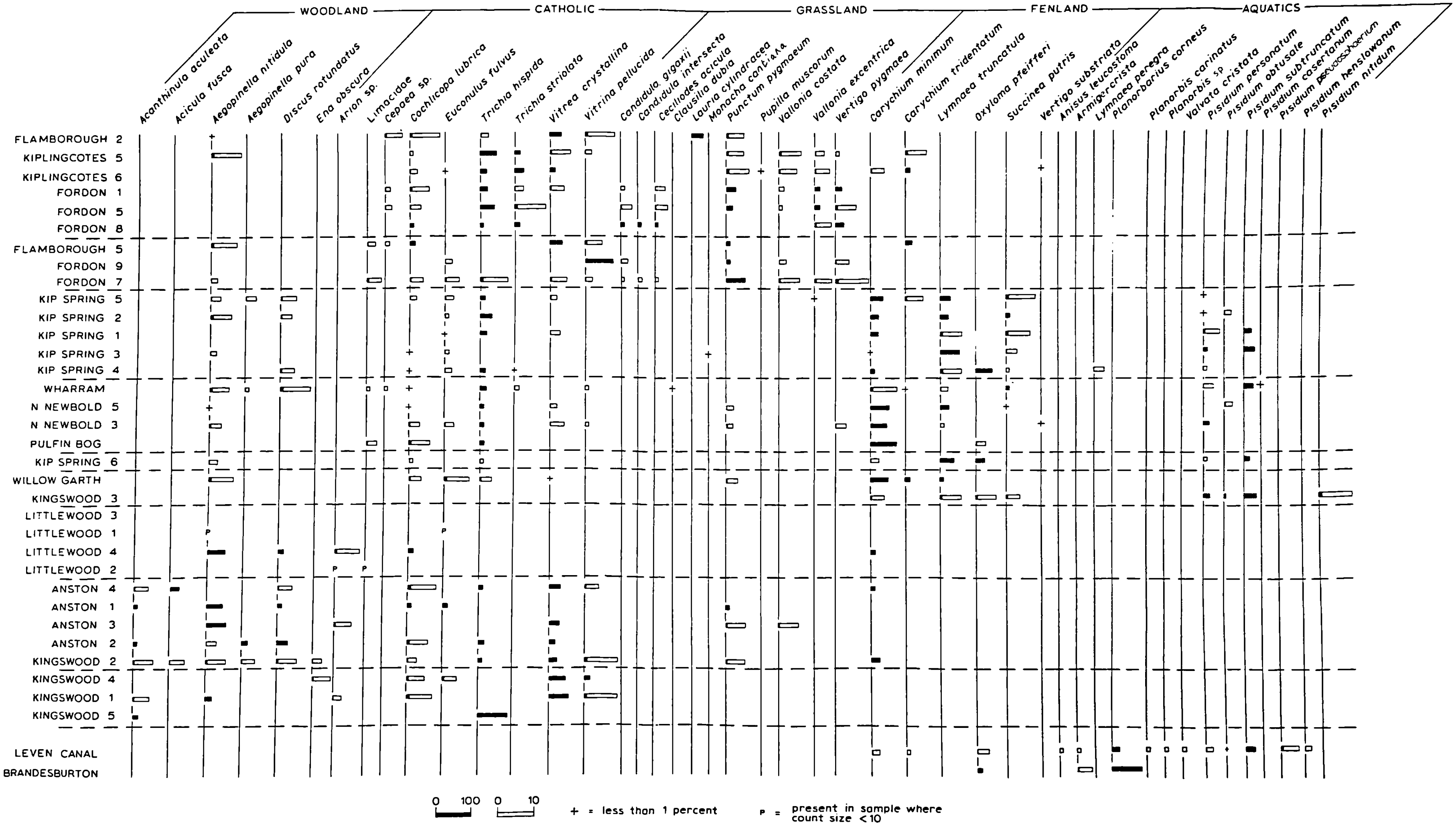


FIG. 5.10 MOLLUSC PERCENTAGES FROM MODERN ANALOGUE SITES.

BROKEN LINES INDICATE TWINSPAN GROUPINGS OF SITES BASED ON HERB DATA.

collapse to form a dense mat. Other grasses present in this community included: *Dactylis glomerata*, *Poa annua* and *Festuca ovina*. Only tall forb species could survive amongst the *B. pinnatum*, e.g. *Heracleum sphondylium*, *Centaurea nigra*, *C. scabiosa* and *Ononis repens*. A few hawthorn, the remnants of an old hedge, lay within 20m of the quadrats; other than these the nearest arboreal taxa lay approximately 300 m away.

The pollen influx to these sites was low with 970 grains $cm^2\ y^{-1}$ recorded from site 6, which is slightly less than the lowest influx recorded for prairie grassland by M.B.Davis *et al.* (1973). Despite the distance to the nearest woodland both samples had 7 arboreal pollen taxa represented, one of which was *Tilia*. Seven herb taxa were recorded in the quadrat at site 6, and 9 at site 5; of these 4 were represented in the pollen record for each site. A further 7 herbaceous taxa were recorded at site 6 and 10 at site 5. The pollen likely to have been derived from within the chalk grassland was 90% to 91% of the total pollen influx. The commonest vegetation types were all well represented in the pollen spectrum and the Gramineae vegetation percentage of *c.* 90% was matched by peaks of 62% and 82% in the pollen assemblage.

The fruit assemblages recorded Gramineae at frequencies of 72% and 46.5%. The fruits, but no pollen, of *Fumaria officinalis* were recorded from both sites. Plants of *F. officinalis* were not found within the quadrats but were abundant in the surrounding vegetation. The seed concentration was higher at site 5 than at site 6 with values of 576 and 102 fruits per litre respectively, which represented the same relative pattern of deposition as found in the pollen influx.

Only two of the vegetation taxa present in site 5, Sanguisorba minor and Vicia sp., were absent from both the pollen and propagule assemblages. These two taxa were infrequent members of the community representing only 3.5% of the recorded contacts.

No bryophytes were recorded from these sites.

The molluscan assemblage was uniform at both sites with 12 species present at a concentration of 220 mollusc shells per litre of soil. The composition of the assemblage was typical of open habitats with such species as: Vallonia costata, Vallonia excentrica and Pupilla muscorum. These, although strong environmental indicators, were outnumbered by the catholic species such as Trichia hispida, T. striolata, Vitrea crystallina and Cochlicopa lubrica. The catholic species represented over 65% of the mollusc fauna at each site.

5.6.3 Forb-Rich Chalk Grassland

Three pollen traps were recovered from the open species rich areas of Fordon Chalk Bank (1, 5 & 8). The vegetation was a short sward; rabbit and cow dung indicated the presence of grazing animals. A variety of grasses were present including: Festuca ovina, F. rubra, Poa annua, Koeleria cristata, Briza media and Arrenatherum elatius. As this group cannot be separated on their pollen, in the vegetation survey they were recorded simply as Gramineae. Similarly the sedges Carex hirta, Carex flacca and Carex panicea were common in the grassland; these were amalgamated to Cyperaceae. Amongst the grassland were dense patches of *Helianthemum chamaecistus*, *Thymus praecox* and *Sanguisorba minor*. *Filipendula vulgaris*, *Pimpinella saxifraga*, *Linum catharticum*, *Scabiosa columbaria* and *Centaurea scabiosa* were locally abundant. To the north the chalk bank was bounded by a hedge in which *Crataegus monogyna* was the commonest shrub. Scattered specimens occurred throughout the reserve, as did clumps of *Ulex europaeus*. In the middle of the reserve there stood a copse of *Fraxinus excelsior*. The pollen traps were set at least 50 m from the copse in order to minimise arboreal pollen input.

The mean pollen influx to the traps was 2922 grains cm^{2} y^{-1}. Chalk grassland is characteristically a species rich association but the palynomorphs produced by the plants of this community are often only identifiable to a family or group level. Thus in the forb-rich chalk grassland of Fordon Chalk Bank the maximum number of palynologically separable taxa recorded in a 5 m radius survey area was 24, and the minimum 11.

Gramineae which had scores of 37% to 75% from the vegetation survey had values of 33% to 43% in the pollen data. At Fordon 1, 21 species were recorded in the vegetation survey and yet only 6 of these were present in the pollen assemblage. This was an anomalously low figure but perhaps reflected an abundance of relatively rare species or an abundance of poor pollen producing species. If the representation of those 15 unrecorded taxa in the vegetation assemblage is taken into account it may be seen that they totalled less than 9% of the contacts along the transects (Fig. 5.6). The other two sites both had over 50% of the adjacent flora represented in the pollen record. Although the lowest figure for the representation of the adjacent flora was 54% the percentage which was derived from within the habitat as a whole was consistently over 90%. The local flora consisted of localised clumps of species and the winds blowing across the bank may have produced a relatively homogeneous pollen distribution. This would not necessarily replicate the balance of the adjacent vegetation.

Pollen derived from outside the habitat was composed primarily of arboreal taxa (6%) and Cerealia (2%).

The seed assemblages had a range of concentrations from 300 to 500 fruits per litre and a species diversity of 11 to 14 taxa. Gramineae were represented in these samples with values of 6% to 11%; this taxon was apparently under-represented. Gramineae caryopses have been found to be relatively rare in fossil sediments (GreatRex, 1983) and it was suggested that this may have been due to selective predation and poor fossilisation. Alternatively, perhaps wild grasses, particularly in grazed environments, are poor seed producers in relation to their cover abundance.

The seeds of one sample were dominated by Linum catharticum (33.6%) whilst another was rich in Sanguisorba minor (24.4%) and the third presented a blend of these two species plus Helianthemum chamaecistus and Ranunculus sec Ranunculus as the dominant components of the propagule assemblage. The fruit record reflected the local dominance of broad leaved forbs more accurately than the pollen. Campanula fruits were recovered from all the soil samples and yet no *Campanula* sp. was recorded for these sites in the vegetation survey, although both *C. rotundifolia* and *C. glomerata* were present in the surrounding grassland. Unless flowering at the time of the survey these plants could easily be overlooked because the narrow, inconspicuous stem leaves may be missed amongst the leaves of grasses. *Linum catharticum* is another species often under-represented in surveys (C.Smith, 1980) and the total of 26.5% for the fruits of this species, in a plot where no *Linum* spp. had been recorded, almost certainly indicates that this plant had been overlooked in the survey.

Apart from the species which were missed in the survey *c.* 90% of the fruits could have been derived from plants growing within 5 m of the sample site. The representation of the adjacent flora afforded by the fruits was *c.* 97% to 100%.

The bryophytes of these samples were *Plagiomnium affine*, *Mnium punctatum*, *Hypnum cupressiforme*, *Fissidens taxifolius* and *Eurynchium* sp..

The concentration of mollusc shells in the soil samples was low at 50 to 130 per litre of soil. There was however a reasonable diversity of taxa with a total of 13 species from this habitat (Fig. 5.10). The samples were relatively uniform in their composition with a range of species characteristic of open grassland habitats, e.g. *Candidula gigaxi*, *C. intersecta*, *Vallonia costata*, *V. excentrica* and *Pupilla muscorum*. The Blind Snail, *Cecilioides acicula*, was found in each sample. This species would not normally be found on the soil surface and is generally only found there as the result of soil disturbance by burrowing animals such as moles, or palaeoecologists. The presence of *C. acicula* indicates a permanently dry, aerobic soil environment. The mollusc species listed above were the environmental indicators, but there were also members of the assemblage which show no strong environmental preference such as *Trichia hispida*, *Cochlicopa lubrica* and *Vitrea crystallina*. These catholic species are ubiquitous, but in these samples their numbers were evenly balanced with those of the chalk grassland indicator taxa.

5.6.4 *Ulex* Scrub on Chalk Grassland

Three pollen traps were left in stands of *Ulex europaeus*, which might seem a high proportion compared with other non-woodland habitats, but this is a function of their survival. Whereas 30 traps were set in non-woodland locations and 12 were recovered, all three traps set in the *Ulex* clumps survived. The sites all had *c.* 70% to 78% values for *Ulex europaeus* cover, although each represented a slightly different habitat.

At Fordon 7 the *Ulex europaeus* was growing as a woodland edge plant on the margin of the *Fraxinus excelsior* copse. The trap was set so that it was about 1 m into the grassland and almost overhung by the *Ulex*. The grassland was rich in *Thymus praecox*, *Sanguisorba minor* and *Helianthemum chamaecistus*. The woodland, although dominated by *Fraxinus excelsior*, also contained *Crataegus monogyna* and *Sambucus nigra*. Fordon 9 was set in the middle of an isolated clump of gorse some 10 m across which was surrounded by chalk grassland. Within the clump there were some scattered grasses but otherwise it was an almost uniform mass of *Ulex*. At Flamborough 5 the *U. europaeus* was part of a sprawling *Ulex* - *Rubus* scrub amongst which small patches of chalk grassland occurred. *Sanguisorba minor* was present in small numbers but the commonest of the broad leaved forbs was *Centaurea nigra*.

The pollen influx to these traps varied markedly. The two Fordon sites had pollen influx values of *c.* 1400 grains cm^2 y^{-1}, whereas the trap at Flamborough had an influx of 9500 grains cm^2 y^{-1}. The effects of grazing at Fordon Chalk Bank might be the cause for this disparity.

Ulex europaeus was consistently under-represented in all these samples with values ranging from 1.5% at Flamborough to 18.8% at Fordon 9. In terms of pollen influx this represented a range of 37 to 247 grains cm^2 y^{-1}. This is probably best explained by the entomophilous nature of this species. As the pollen representation of this taxon was so low the other species were over-represented by the percentage data.

Fordon 7 received an arboreal pollen input of 6.8% which did not include any *Fraxinus excelsior* pollen but did include 3.8% *Ulmus*, a tree which was not recorded in the copse. The lack of *F. excelsior* pollen goes some way to corroborate the suggestion made in chapter 3 that 1983 was a bad flowering year for *Fraxinus* on the Yorkshire Wolds.

Of the 11 vegetation taxa present at Fordon sites 7 and 9, 9 and 6 taxa, respectively, were represented in the pollen rain from those sites. Those taxa not represented accounted for less than 2% of the vegetation cover.

At Flamborough the pollen record accounted for 7 out of 13 species, the 6 unrepresented species accounted for 6.3% of the vegetation sum. 5.8% of this was due to Centaurea nigra, the pollen of which was not recorded from this site although the fruits totalled 70.7% of the propagule assemblage. It is possible that for some reason these plants failed to flower at this site in 1983 and that the seeds were from the seed bank in the soil which may have been accumulating for a number of years. No U. europaeus seeds were found in this sample despite the close proximity of the bush. The sample from Fordon 7 contained only one Ulex europaeus seed and at Fordon 9 this species accounted for only 14% of the propagule total. The propagules of this plant are relatively large and the flowers each produce just one pod containing 2 to 6 seeds (Clapham et al., 1962). The seed production of such a plant is much lower in proportion to its size than that of herbs such as C. nigra and Plantago lanceolata. Linum catharticum, Helianthemum sp. and Sanguisorba minor were all important components of the fruit assemblage at Fordon 7 where these three species made up 82% of that assemblage. At Fordon 9 the vegetation in the middle of a gorse clump was less dense and contained a less diverse flora. Gramineae and Myosotis represented 66.7% of the seed total whilst large fruit stones of Crataegus monogyna and Rubus fruticosus agg. represented 3% of the total. These seeds were probably sown by frugivorous birds using the isolated gorse clump as a perch or roosting site.

The scarcity of Ulex seeds offered the opposite problem to that of the over-representation of birch fruits recorded by

GreatRex (1983). She suggested that one way to compensate for this would be to count the Betula bud-scales rather than the fruits. Perhaps the needles of gorse should be recorded, as these were abundant, readily identifiable, and might give a better representation than either the seeds or the pollen.

The bryophytes from Fordon 7 and 9 were: Fissidens taxifolius and Mnium affine, Plagiomnium punctatum and Hypnum cupressiforme. At Flamborough 5 only two mosses were found which were Fissidens taxifolius and Hypnum cupressiforme, species which occur in chalk grassland but have a tolerance to light shading.

The molluscan fauna of these Ulex europaeus dominated plots tended towards woodland and shade-loving species. This was best illustrated by Fordon 9, where the open ground species, such as Candidula spp. and Punctum pygmaeum were much reduced in number, whilst the catholic species such as Vitrina pelucida were abundant. In this sample 81% of the mollusc testa recovered were of V. pelucida. At Fordon 7 there was a fauna of an essentially open nature with Punctum pygmaeum (57%), Vertigo pygmaea (9.2%) and Vallonia spp. (10%). This was because the plot, although in the lee of the copse, was still an essentially open ground site and so it favoured the heliophilous taxa. The proximity of the copse would have offered a degree of protection from desiccating winds, and this might explain the abundance of Punctum pygmaeum, a mollusc characteristic of moist, lush vegetation.

At Flamborough 5 the composition of the fauna was similar to that of the north-facing clifftop location of Flamborough 2. It has already been suggested that the aspect of Flamborough 2 might have resulted in an unusually moist and shaded location for an open grassland. The microclimate beneath a gorse bush would be expected to be similarly moist and shaded. This might account for some of the similarity between Flamborough 5 and Flamborough 2. Another influence might be the salt-laden air, as this might preclude the presence of some taxa. The commonest taxa at Flamborough 5 were *Vitrea crystallina*, *Punctum pygmaeum*, *Cochlicopa lubrica* and *Carychium tridentatum*.

5.6.5 Seasonally Flushed Grasslands

The sites around Kiplingcotes spring formed this category. These were grassland areas where there was a strong fluctuation in the local water level throughout the year. In winter a pool *c.* 0.3 m deep stands in the bottom of the hollow. In some years this may not dry out, but in most summers the water level drops, exposing a bare sandy soil. It would appear that very few species were able to grow in this central area as the environment was so extreme. Almost the only plant to colonise this area was *Rumex conglomeratus*, which grew in scattered clumps. Plants characteristic of permanently wet sites were absent, although a few drought-resistant fenland taxa fringed the pool margins, e.g. *Scrophularia aquatica*, *Potentilla palustris* and *Berula erecta*. The slopes of the hollow were rough pasture containing *Festuca ovina*, *Deschampsia cespitosa*, *Phleum pratense*, *Centaurea nigra* and *Heracleum sphondylium*. At the break of slope in the base of the hollow there was a mosaic of different vegetation types with stands of *Epilobium hirsutum*, *Cirsium arvense* and *Scrophularia aquatica*. The vegetation on the eastern side of the hollow was dominated by Urtica dioica on the drier ground. In the wetter areas this association gave way to a mixture of sedges, fine grasses and broad leaved herbs, e.g. Veronica chamaedrys, Potentilla palustris, Galium verum and Equisetum palustre.

The pollen influx to this site ranged from 4200 to 18000 grains cm^2 y^{-1}. Of this, 96% to 98% was estimated to be locally derived and 50% to 95% could have been of adjacent origin. In all cases over 50% of the herb taxa recorded within 5 m of the sampling points were represented in the pollen diagram. Gramineae was usually the dominant pollen type with values as high as 94%. Gramineae pollen appeared to be consistently over-represented as the vegetation survey values for this group never exceeded 78%. The other herb taxa were consequently under-represented, but even allowing for this there were some anomalous results. Epilobium was not recorded from a sample in which this taxon attained 42% of the adjacent vegetation cover. Cirsium was also strongly under-represented with a vegetation cover value of 18% and a pollen value of less than 1%. The species which were not recorded in the pollen data, but were present in the adjacent vegetation, represented as much as 45% of the cover.

It would appear from this that the mosaic of vegetation in the bottom of the hollow was too fine to be accurately reflected in the pollen rain. Possibly the effect of the grasslands on the slopes and in the adjacent fields was to contribute a high pollen influx of Gramineae and dry land taxa to the site, which masked the small scale variations in the wetland taxa. This might also explain the apparent over-representation of Gramineae in the pollen rain.

The pollen influx to this site was the highest of any recorded in this survey. The shape of the catchment may have played some part in this forming a natural eddy in which pollen deposition took place, or it could be related to the exclusion of grazing animals from this site. Rabbits were present but not in sufficient numbers to produce a short sward and thus the grasses were able to flower and set seed. That the lack of grazing might have been an important element in this influx would be supported by the high concentrations of fruits (562 to 1630 per litre of soil) recorded from this site.

The seed data showed a stronger bias towards the adjacent vegetation. The proportion of adjacent vegetation taxa represented within the seed data ranged from 50% to 89% and species such as Cirsium arvense and Epilobium hirsutum were recorded, even though still under-represented. Nasturtium microphyllum was consistently over-represented in the propagule data, although it only occurred in the propagule assemblages of sites where it was recorded in the vegetation data. An example of this was where the plant was present with a vegetation cover of 1.7%, whereas the fruit representation was 48%. This of course does not make any allowance for previous years in which the plant may have flowered profusely and built up a rich seed bank in the soil. Urtica dioica, which was a relatively rare component of the pollen counts, was well represented in the propagule data, with a tendency to being over-represented where dense stands of it occurred. A clump of U. dioica recorded as 3.2% of the vegetation cover was represented by 18% of the total seed assemblage. Gramineae were generally under-represented with values from 11% to 54%.

The bryophyte flora was sparse with only three species recorded: *Diacranoweisia cirrata*, *Amblystegium tenax* and *Hypnum cupressiforme*. These mosses are resistant to seasonal inundation but were probably not growing *in situ* as *A. tenax* and *D. cirrata* both grow on either a trunk or bare rock substrate (Smith, 1978). These taxa may have been washed into the deposit by floodwater or slope wash.

The mollusc assemblages were rich with 300 to 500 testae per litre from as many as 14 taxa. The assemblages collected at each site were of an essentially similar nature with a mixture of damp ground species of wide environmental tolerances, e.g. *Euconulus fulvus* (2%) and *Cochlicopa lubrica* (2%), through obligate hygrophiles e.g. *Carychium minimum* (1% to 34%) and *Succinea putris* (3% to 10%), to the truly aquatic species such as *Lymnaea truncatula* (23 to 55%). In sample 3, 70 *Pisidium* shells were found; as there were no living animals in this group it may be that they reflect a wetter period in the past when *Pisidium* colonised the pond. An alternative explanation may be that this was a point of natural deposition where winter flood waters from the adjacent stream deposited shells. The presence of *Discus rotundatus*, a woodland mollusc, *Vallonia excentrica*, a heliophilous mollusc, plus the wetland and catholic taxa, all in one sample, would argue for a certain degree of secondary transport and deposition.

5.6.6 Fen Meadows

The fen meadows of this survey included 2 quadrats in areas flushed by chalk springs, one straddling a stream which ran through an 'improved' pasture, and one in wetlands flushed by water from the River Hull. Although the water of the R. Hull was greatly enriched by nutrients from arable and fish farming waste, the fen at Pulfin Bog did not appear to have been affected by it. A strong floral similarity existed between the spring flushes of North Newbald and the backwater fen of Pulfin Bog. The streamside at Wharram Percy supported a less diverse flora and was isolated by the DECORANA analysis, implying a considerable ecological dissimilarity from the other wetland and grassland sites; hence, this site is dealt with separately.

5.6.7 Enriched Flushed Grassland

The stream below the dam at Wharram Percy formed the divide between a field of improved pasture to the east and a slope of rough grassland to the west. A single large ash tree, with a girth of 2 m, was the only tree within 20 m of the sampling point. A few Crataegus monogyna were scattered along the banks of the stream but the nearest dense stand of trees was a grove of young willows around the dam. There was also a mature plantation of Fagus sylvatica, Picea abies and Larix decidua about 0.5 km to the south east.

The flora of the centre of the stream was dominated by Apium nodiflorum. Towards the edges Rumex spp., Epilobium hirsutum, Filipendula ulmaria and Equisetum palustre formed a tall herb community on the western side, whilst on the eastern side, where the pollen trap was sited, there was a short species-poor grassland community. The grassland had been seeded with Lolium sp. and this highly competitive perennial grass had ousted most of the broad leaved forbs leaving just Cyperaceae (1%), Ranunculus acris (<1%), Galium verum (6%) and Lathyrus pratensis (<1%). Gramineae represented 60% of the contacts in the vegetation survey. Also present in the quadrat though not on any of the transects were clumps of Plantago lanceolata and Caltha palustris.

The pollen influx to this site was 4170 grains cm^2 y^{-1}, which was made up of 33 pollen taxa, 7 of which were arboreal taxa (8.2%). Despite the presence of the mature specimen of Fraxinus excelsior no pollen of this taxon was recorded in the pollen rain; this was commented on in chapter 3.

Of the herb taxa the most abundant were Plantago lanceolata (44.9%) and Centaurea nigra (11.8%) neither of which were recorded in the vegetation survey. The low pollen influx of Gramineae (470 grains cm^2 y^{-1}) might indicate that the effects of grazing combined with the sowing of a hybrid grass had reduced the adjacent pollen influx. The ungrazed grasslands of the valley slope to the west may have been contributing a high proportion to the pollen rain.

The seed assemblage at this site was quite rich with 744 fruits per litre of soil. Centaurea nigra and Plantago lanceolata were both absent from this assemblage suggesting that the pollen had indeed been derived from a non-local vegetation source. Gramineae (22.9%), Cyperaceae (15.3%) and Apium nodiflorum (42%)

were the most abundant of the fruit types. Of the nine vegetation taxa recorded (Equisetum is discounted from this total as its propagules are included in the pollen data) eight were represented in the propagule assemblage; only Lathyrus pratensis was absent. Thus >99% of the vegetation cover was represented in the seeds total and these species accounted for 98.6% of the propagule sum.

The only bryophyte recorded from this site was Amblystegium varium which is a lax moss commonly found in fens and along the sides of streams.

The molluscan assemblage from this site had a concentration of 530 shells per litre of soil, and was species-rich with 17 species present. Most were moisture-loving species, e.g. Succinea putris (10%) and Carychium minimum (8%). There were also truly aquatic species such as Pisidium (30%) and Lymnaea truncatula (2%), and some characteristic of moist shaded environments, Aegopinella nitidula (6%), Clausilia dubia (1%) and Discus rotundatus (9%).

5.6.8 Rich Fen Meadows

Of the three sites, North Newbald 3 and 5 and Pulfin Bog, the latter was the wettest. At North Newbald there was a series of springs with Juncus effusus and J. inflexus crowding their margins. The land between the springs became progressively drier to the mid-point where the most abundant taxa were Epilobium hirsutum, Filipendula ulmaria, Urtica dioca, Cyperaceae and Gramineae. In the intermediate areas grew Mentha aquatica, Menyanthes trifoliata and Rhinanthus minor. Where water ponded up localised flushes of wetland plants formed, e.g. Pulicaria dysenterica, Geum rivale, Cardamine pratensis and Nasturtium aquaticum.

The only trees near to these sites were Salix sp., but these were at least 50 m distant at North Newbald, although at Pulfin Bog a small copse of Salix cinerea was present on the edge of the 20 m quadrat area.

North Newbald 3 was at the margin of one of the temporary pools; 27 herb taxa were recorded in which Gramineae (51%) was by far the commonest component. Festuca rubra, Holcus lanatus and Agrostis stolonifera were the commonest grasses, with Poa spp. on the drier hummocks. North Newbald 5 was an area rich in Carex ovalis and Carex disticha; here the Cyperaceae totalled 48% of the vegetation cover and Gramineae were reduced to 34%.

The pollen influx to these two sites was c. 3000 grains cm^2 y^{-1} and of the 27 taxa recorded in the vegetation at North Newbald 5, 12 were recorded in the pollen rain from that site. A higher proportion, 16 out of 28, were recorded from site 3. Pollen of Juncus was not recorded from either of these samples although locally abundant. This could almost certainly be ascribed to the fragility of the pollen. The proportion of Gramineae recorded in the vegetation survey was accurately reflected by the pollen spectra from these sites. c. 85% of the local flora had some representation in the pollen spectra, and of the 15% which went unrepresented Juncus accounted for 10%.

High concentrations of fruits existed in both the North Newbald samples (1250 to 2000 fruits per litre) and 15 to 18 taxa were represented. At both sites >99% of the seeds could have been derived from within 5 m of the sample site, which agrees well with the data obtained by GreatRex (1983) in which she found that as many as 99% of the seeds could have been derived from species within 5 m of the sampling point in Scottish fen communities. Although North Newbald 5 had fewer than 50% of the taxa from the surrounding vegetation represented in the seed assemblage, those present accounted for >90% of the vegetation cover. The only notable absentee was Nasturtium aquaticum, which would seem to be a prolific seed producer and yet in this case was absent. This may have been because the plants were growing in a pool; spring-fed streams flowed through the pool and these would create sufficient flow to carry the seeds away from the sample site.

In the site at Pulfin Bog there was a slightly less diverse flora with 15 vegetation taxa, the commonest being Cyperaceae (56.5%), Galium aparine (21%) and Gramineae (11%). Wetland species such as Angelica sylvatica, Lemna minor and Valeriana dioica were also present.

The pollen influx to this site was the lowest of all (790 grains cm^2 y^{-1}). This rate is so low that it must be questioned as to whether the trap was functioning properly throughout the year. Cyperaceae were under-represented in the pollen rain with just 4.2% of the total herb count whilst Gramineae were over-represented with 67.4%. Again this is probably a reflection of a relatively small area of vegetation having its local pollen production swamped by that of the extra-local or regional pollen rain.

Of the 18.3% arboreal pollen input at Pulfin Bog only a third was from Salix, the only tree which grows on the fen. An ancient hedge along the eastern side of the reserve contained Quercus but this was at least 100 m distant and would not account for the presence of Betula and Pinus which made up almost half of the arboreal pollen total.

The seed concentration at this site was the highest recorded from a site without Betula, with 2250 seeds per litre. Cyperaceae nutlets were abundant with 34.6% and Gramineae was reduced to 4.3% of the total. Of the 15 vegetation taxa present 10 were represented in the propagule assemblage. Again it was shown that palynological evidence provided a good overall impression of the regional vegetation, the almost treeless landscape of an extensive reedbed, but it was the seeds and fruits which gave by far the most accurate and detailed description of the local vegetation.

The bryophyte flora of these habitats included Plagiomnium elatum, Hypnum cupressiforme and Amblystegium varium.

The concentration of mollusc shells ranged from 130 per litre at Pulfin Bog to 580 per litre at North Newbald 3. All the samples were dominated by the obligate hygrophile Carychium minimum with values of 48% to 76%. Trichia hispida was the commonest of the catholic species and at North Newbald 3, 15% of the total were Pisidium spp.. Oxyloma pfeifferi was identified from Pulfin Bog, a mollusc indicative of an unshaded, wet environment.

5.7 MODERN ANALOGUE DATA FROM WET VALLEY WOODLANDS

5.7.1 Alnus Woodland

Willow Garth and Kingswood 3 are treated together, as these both showed stages in the succession from valley fens towards dry valley woodlands. The dry fen and damp woodland of Willow Garth contrasted with the lake margin woodland carr of Kingswood 3, which showed an earlier stage in the same succession. The dominant tree at Willow Garth was Alnus glutinosa, accounting for 41% of the canopy; Salix fragilis and Populus alba were locally abundant with 16% of the canopy. At Kingswood Alnus glutinosa formed 44.7% of the canopy near the lake margin. Often the alder trunks had collapsed and the trunks hung out over the lake. The shoreline was lined with Euonymus europaeus and Taxus baccata (2.3%). On the slightly higher ground of the valley sides Fagus sylvatica (46.3%) and Fraxinus excelsior (5.6%) were the commonest trees. T. baccata grew on the hillslopes and, of the dry land taxa, it extended the furthest towards the fen edge. The width of this fen was only about 12 m, large enough for the vegetation quadrat to lie within it, but the arboreal survey (20 m radius) took in some of the trees growing on the drier slopes and much open water. The high value for Fagus sylvatica was a reflection of its dominance on the local hillside although it was entirely absent from the fen. The ground flora of these two sites reflected a marked difference in their seral state. At Kingswood, Nasturtium aquaticum, Mentha aquatica and Caltha palustris were common species, totalling 40.3% of the vegetation cover. These species were all present at Willow Garth, not in the quadrat area, but growing in the drain which flowed 15 m to the south of the quadrat. Gramineae were present in the vegetation at both sites. At Willow Garth the dominant grass was *Phalaris arundinacea*. At Kingswood there were nearby stands of *Phragmites* sp., plus, on the landward side, woodland species, e.g. *Melica uniflora*. Grasses were not the dominant herb vegetation at either site with 7% at Kingswood and 15.7% at Willow Garth. At Willow Garth an open area just to the east of the sample site had been created by windblow; this was now dominated by *Filipendula ulmaria* and *Epilobium hirsutum*. Under the shade of the trees which overhung the sample site, this dominance was reduced to 17% for *F. ulmaria*, and *E. hirsutum* was completely absent. *Galium aparine* was a common plant in all the open areas at Willow Garth, forming dense mats around the bases of the taller herbs. On the sample site a stand of *Iris pseudacorus* (9%) was entangled in *G. aparine* (36%). *Urtica dioica* grew in dense stands at Willow Garth. Such a stand formed the western margin of the ground flora survey giving *U. dioica* a score of 25%.

The pollen influx to the site at Willow Garth was 3600 grains cm^2 y^{-1}, which would be considered low for a woodland habitat. 50% of this influx was made up of *Filipendula ulmaria*, which represented 69% of the herb pollen sum. The likelihood that this was an anomalously high value due to the direct input of an anther to the trap is reduced when it is considered that a similarly high value was obtained from three moss polsters, collected from Willow Garth, as part of the preliminary study (Fig. 5.5). It would seem that much of the pollen input came from the open unshaded area where *F. ulmaria* was the dominant plant. Of the pollen sum, 28% came from trees and shrubs, and Gramineae contributed a further 6.5% of the total (9% of the herb total). Iris pseudacorus was not recorded in the pollen analyses, nor were Equisetum or Angelica sylvatica. This resulted in 24% of the vegetation having no representation in the pollen analysis. Of the pollen sum 74% could have been derived from within 5 m of the sample site.

The arboreal pollen input to Willow Garth represented 23% of the pollen sum. Of this Salix (7.2%), Populus (3.9%), Betula (3.9%) and Alnus (2.4%) were the most abundant taxa. The apparent dominance of Salix does not represent the local balance in the quadrat, but an overgrown osier bed to the west of the sample site may have been contributing to the pollen sum. Willows actually overhung the trap but these were all shoots from a fallen female tree and so would not contribute to the pollen influx. Betula pollen was clearly over-represented as there was only one birch tree in the reserve and that was some 50 m away through fairly dense woodland. This percentage would seem to be as likely to represent a regional Betula pollen input as the production of one tree. Alnus glutinosa was poorly represented in this data set and this might again reflect a stand of woodland too local to be adequately represented in a pollen data set.

The data from the propagules at Willow Garth revealed a concentration of 410 fruits per litre of soil, of which 33% were Alnus glutinosa, 5.3% were Salix or Populus capsules and 25% were of Filipendula ulmaria (40% of the herb propagule total). Of seven vegetation taxa recorded in the herb flora, six were represented in the seed assemblage (Fig. 5.9).

At Kingswood 3 the pollen influx was c. 8000 grains cm^2 y^{-1}, in which there were 36 pollen and spore taxa. Of these, 19 were non-arboreal species, 6 of which could have been derived from the adjacent vegetation, leaving 10 taxa present in the adjacent vegetation with no pollen representation. The representation of the pollen types could be re-stated as 40% which could have been adjacently derived, 96% which could have been derived from the local vegetation and 4% from a non-local, e.g. arable, landscape. As this site did not lie within a homogeneous vegetation type the pertinence of these values is questionable. Probably the most useful is the estimate of the maximum amount of pollen which could have been derived from the adjacent vegetation (40%) and its reciprocal, the proportion of adjacent vegetation, which may have some representation in the pollen data (51%). These values were low, suggesting that there was a relatively high influx of pollen from a wider region. This might be expected in a valley, where pollen from the adjacent hillsides is likely to drift down into the valley bottom. Few aquatic taxa were recorded, as their pollen would be primarily water-borne and the trap showed no sign of having been flooded.

Gramineae were recorded in the vegetation with a value of 7.1% but the pollen influx of this taxon was only 571 grains cm^2 y^{-1}. This was lower than the 1135 grains cm^2 y^{-1} obtained from Kingswood 5, a dense Tilia-Taxus dominated woodland, in which no Gramineae was recorded. This may have been due to the reduced effect of the pollen production of grasslands surrounding the Kingswood because Kingswood 3 was more centrally located within the woodland than any of the other sites. The Gramineae were still over-represented, but not to the same extent as in the other woodland sites.

The arboreal pollen input to Kingswood 3 represented 44% of the pollen sum of the taxa. Included in this total were Betula (5.6%), Pinus (2%) and Salix (4.8%), none of which was recorded within the quadrat. Alnus pollen accounted for 11% of the total and 25% of the arboreal pollen total. Taxus attained 5.8% of the total pollen input, c. 12% of the arboreal pollen sum. Both Fraxinus (1.4%) and Fagus (<1%) were grossly under-represented, which supported the view of Andersen (1973) that these taxa were poor pollen producers.

The propagule concentration was 610 fruits per litre of sediment. 15 taxa were represented, of which 4 were present in the adjacent herb flora. The commonest fruit was that of Alnus glutinosa (31%) which had a concentration of 190 fruits per litre even though the nearest specimen of this tree was 15 m away. The fruits of A. glutinosa were shown to float for up to 12 hours due to their corkiness (McVean, 1953) and so it is not unlikely that this assemblage represents a mixture of fruits which have blown and drifted into the sediment. The sample contained 9.8% Betula fruits, although no Betula was recorded in the vegetation of this plot. It is common to see the winged fruits of Betula floating on the surface of ponds in the autumn and so it is possible, that like the Alnus, these may have been washed into this deposit. Another well represented arboreal taxon was Taxus baccata, 25 seeds (6%) of this tree were found in the deposit. These had most likely been derived from a large specimen of *T. baccata* which was growing within 5 m of the sample site. Other seeds, e.g. *Crataegus monogyna*, *Rubus idaeus* and *Sambucus nigra*, which all occurred at <1%, may have been bird sown.

The lakeside sediments also contained some of the fruits of semi-aquatic taxa, such as: *Lycopus europaeus* (2.8%), *Cardamine* (14%) and *Carex* (2.1%). One arable weed species present in the assemblage, *Aethusa cynapium*, may have been bird sown, or carried in by the inflow stream.

The bryophytes of these sites were sparse with *Climacium dendroides* being recorded from Kingswood 3 and *Eurynchium* cf. *praelongum* from Willow Garth. Both of these species represent shaded rather than wetland habitats, and the *C. dendroides* may have fallen into the sediment rather than have been growing *in situ*.

The concentration of mollusc shells ranged from 80 per litre at Kingswood 3 to 350 per litre at Willow Garth. In the sample from Kingswood 3, 5 taxa were present all of which were obligate hygrophiles, e.g. *Pisidium* spp. (79%), *Oxyloma pfeifferi* (6%), *Lymnaea truncatula* (6%), *Succinea putris* (4%) and *Carychium minimum* (4%). At Willow Garth there was a greater diversity of mollusca with 9 taxa recorded. The commonest taxa were: *Carychium minimum* (50%) and *C. tridentatum*. *C. minimum* shows a stronger preference for damp sites but these two species are often found together (Kerney and Cameron, 1979). Also found at Willow Garth was *Lymnaea truncatula*, a species which, although aquatic, can withstand sustained periods of drought. Its presence indicates that the site is still waterlogged and probably subject to periodic flooding. The other 6 species show no marked habitat preference, being catholic species with a general tendency towards moist, shaded environments.

5.7.2 Salix Woodland

Peterken (1981) did not recognise Salix sp. as forming woodlands in their own right but regarded them as a subdivision of the wet valley alderwoods. Whereas the alder woods previously considered were mature woodlands, albeit gradually changing, the Salix copse at Kiplingcotes Spring was a relatively young wood. As the hollow of Kiplingcotes Spring was probably created as a quarry for chalk, it almost certainly post-dated the nearby railway which was built in the mid-nineteenth century. It is unlikely that a woodland could have withstood such an upheaval, suggesting that the copse is not older than c. 140 years.

The copse lined the outflow stream from Kiplingcotes Spring and extended for about 50 m to where there was a confluence with another, larger, spring fed stream. The ground flora beneath the willows consisted of seven species, two of which were dominant in that community, Berula erecta (57%) and Myosotis sp. (37%).

The pollen influx to this site was 4200 grains $cm^2 y^{-1}$. This is low for a woodland, but as Salix spp. are generally under-represented in pollen diagrams such a result might be expected. Only 5.8% of the pollen total were attributable to Salix, which suggests that these trees were not flowering heavily. Several reasons could be put forward for this. Firstly, that the trees could be predominantly female; in which case a high pollen yield would not be expected. This would seem unlikely as the trees were not regrowth from fallen trunks, and so there was an equal chance of male and female trees occurring in the copse. Secondly that the local environmental conditions were too dry for their growth. This also seems improbable as even in July, when the vegetation survey was carried out, the earth beneath the *Salix* was moist. A third possibility is that they were flowering normally, but that the pollen production from a small copse such as this failed to dominate the regional pollen input. This would be supported by the unrepresentative pollen data obtained for the herbaceous species.

Gramineae, recorded in the vegetation survey at 3.8%, was represented in the herb pollen total by 62.3%. *Berula erecta*, which attained 56.7% of the ground flora, was present in the pollen assemblage at less than 1%. Even if the Gramineae were to be excluded, it would still only represent 2.7% of the total. This strongly suggests that the adjacent and local pollen production (for it was a homogeneous cover for the surrounding 20 m) was being dominated by the extra-local and regional pollen input.

The propagule concentration was 1829 fruits per litre of soil, in which there were 15 taxa represented. Of the 7 species in the ground flora, 6 were represented in the propagule assemblage; only *Galium aparine* was missing. In addition to this, the three arboreal taxa local to the site were all represented: *Salix* (64%), *Crataegus monogyna* (1%) and *Sambucus nigra* (2%). The representation of these taxa gave a much more accurate image of the dominance of Salix in the local vegetation than was obtained from the pollen data. The proportions of the very local herbaceous vegetation were also represented more faithfully by the seed assemblage; Berula erecta was 15% of this total and 42.3% of the non-arboreal assemblage. 21 Gramineae caryopses were recovered from this sediment which represented only 5.3% of the non-arboreal seeds. Similarly Myosotis, which was absent from the pollen data (it is such a small grain, 7 x 4 µm, that it may have been lost through sieving), was present in the macrofossil assemblage with 5.5% of total herbaceous seeds.

Nasturtium microphyllum (11.7%) was the only seed type to seem out of place as this plant was not recorded in the vegetation survey. It may have been missed amongst the dense growth of Berula erecta, or the seeds may have come from plants growing in the other stream and have been washed into this deposit by winter flooding.

No bryophytes were recorded from this deposit.

The mollusc concentration from this site was low, 130 shells per litre, and contained just 7 species. Four species present were obligate hygrophiles whilst the other three were catholic species showing some preference for moist shaded environments. The three dominant species were Lymnaea truncatula (40%), Succinea putris (27%) and Pisidium cf. personatum (25%).

5.8 MODERN ANALOGUE DATA FROM QUERCUS WOODLANDS

The ancient woodland of Littlewood provided three habitats relating to Quercus robur-Corylus avellana woodland. These were:

mature woodland, regenerating woodland and parkland.

5.8.1 Mature Quercus Woodland

The mature woodland with associated species such as Malus sp., Ulmus glabra, Acer campestre and Fraxinus excelsior was recorded at plots 2 and 3. In these plots the herb layer was rich in Hyacinthoides non-scripta (48%), Oxalis acetosella (5%) and Dryopteris filix-mas (33%). The grasses of this woodland were Deschampsia cespitosa and Milium effusum; these totalled 37% of the herb flora.

The forest at Littlewood 2 and 3 was made up of Quercus robur (63% to 83%), Betula pendula (3% to 5%), Corylus avellana (2% to 20%) and 8 other species with less than 5% of the canopy cover.

The pollen influx to these sites was 6000 to 8500 grains $cm^2\ y^{-1}$, of which 62% to 71% was an arboreal pollen input. Quercus robur (37.3% to 59.6%) and Betula (19.7% to 62.3%) were important components of the arboreal pollen influx. Corylus was present in both samples at c. 23% of the arboreal pollen sum.

The concentration of fruits and seeds from these samples was 400 to 1600 propagules per litre of soil. Species diversity was low, with 7 taxa from Littlewood 2, and 9 from Littlewood 3. The propagule data from these sites were massively biased towards Betula with values of 98.6% to 100% of the arboreal seeds total. The production of fruits by Betula totally masked that of the other arboreal taxa. Six acorns of Quercus robur were found in 0.5 of a litre of forest soil from plot 2; from the same sample 703 fruits of Betula were extracted. As can be seen from the computer-generated plot of arboreal canopies (see Appendix 4 for flow diagram of program "Forest 5") (Fig. 5.11) the Betula were not centrally located within the quadrat, and yet their propagules totally dominated the assemblage.

Of the 27% to 38% of the pollen which was non-arboreal, 81% to 90% of it could have been derived from the adjacent vegetation. The representation of Hyacinthoides non-scripta was <1%. Gramineae represented 20% to 40% of the non-arboreal pollen which was a reasonable reflection of the 37% Gramineae recorded in the ground cover. Of the 9 palynologically identifiable taxa, 5 were recorded from Littlewood 3 and 6 from Littlewood 2.

The herb vegetation was poorly represented by the propagules with a maximum of 3 species, out of the 8 in the adjacent vegetation, represented in the assemblage. Dryopteris spp. were excluded from the total of local vegetation taxa as they would not be represented in a macrofossil propagule assemblage. However, the greater definition of identification of the seeds allowed a more explicit determination of taxa, such as Oxalis acetosella (27% non-arboreal seeds) and Circaea lutetiana (2.3% non-arboreal seeds). C. lutetiana is separable palynologically from the other Onagraceae, however it was not recorded from any of the sites studied in this survey. Hyacinthoides non-scripta accounted for 14% of the non-arboreal seeds at Littlewood 3 and 60% of this total at Littlewood 2, which is a better representation of the adjacent vegetation than was provided by the pollen record. Gramineae caryopses were

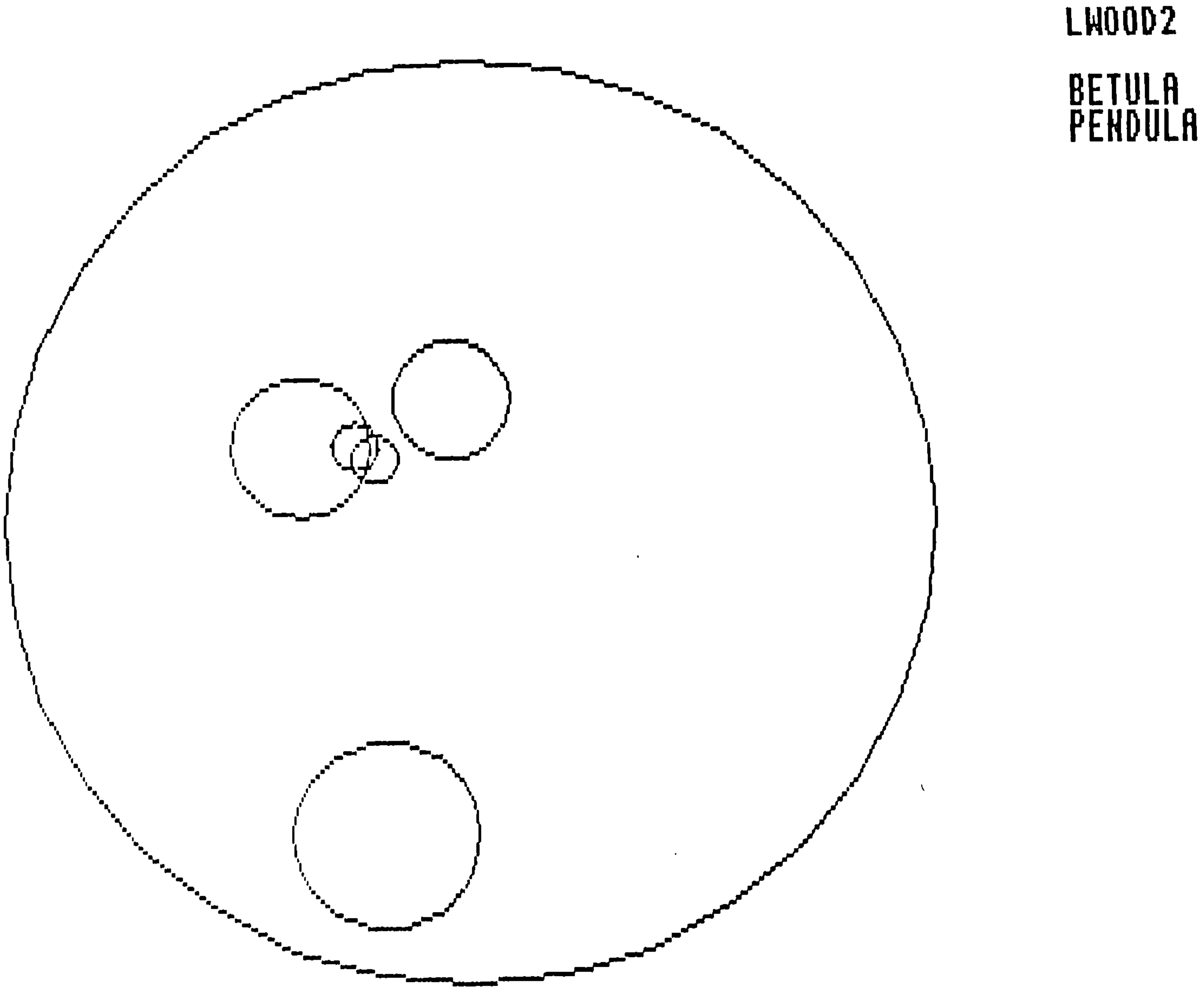


FIG. 5.11 DISTRIBUTION OF BETULA PENDULA CANOPIES AT LITTLEWOOD 2. OUTER CIRCLE MARKS SURVEY LIMIT

recorded only from Littlewood 3 where they represented 46% of the non-arboreal seeds; these were identified as cf. *Milium*.

No bryophytes were recorded from these plots.

The mollusc fauna was depauperate with 2 specimens from Littlewood 2; one was *Arion* cf. *fasciatus* and the other a Limacidae sp.

5.8.2 Regenerating *Quercus* Woodland

At Littlewood 4 there was essentially the same ground flora as found at the previous Littlewood sites. There was, however, a greater dominance of *Dryopteris filix-mas* and also some *Dryopteris carthusiana*. This plot was, however, in a part of the woodland which had been clear felled *c.* 40 years ago. The regrowth was a dense stand of *Fraxinus excelsior* and *Acer pseudoplatanus* (Figs. 5.12 - 5.14). These invasive secondary forest trees form a seral stage in the recolonisation of an oakwood.

The absolute value for the canopy area of Littlewood 3 was *c.* 13000 sq.m., but at Littlewood 4, despite the density of trees the canopy was only *c.* 6000 sq.m.. This was made up of *c.* 140 equal sized individuals. The great majority of these trees were *Fraxinus excelsior* (70% of the canopy area) and *Acer pseudoplatanus* (29% of the canopy).

The pollen influx to this site was 8,600 grains cm^2 y^{-1}, 37.5% of which was of arboreal taxa. *Fraxinus* pollen represented 33% of the arboreal pollen sum, *Acer* just 2% and *Betula* 17%. Neither *Betula* nor *Quercus* (10% arboreal pollen) were

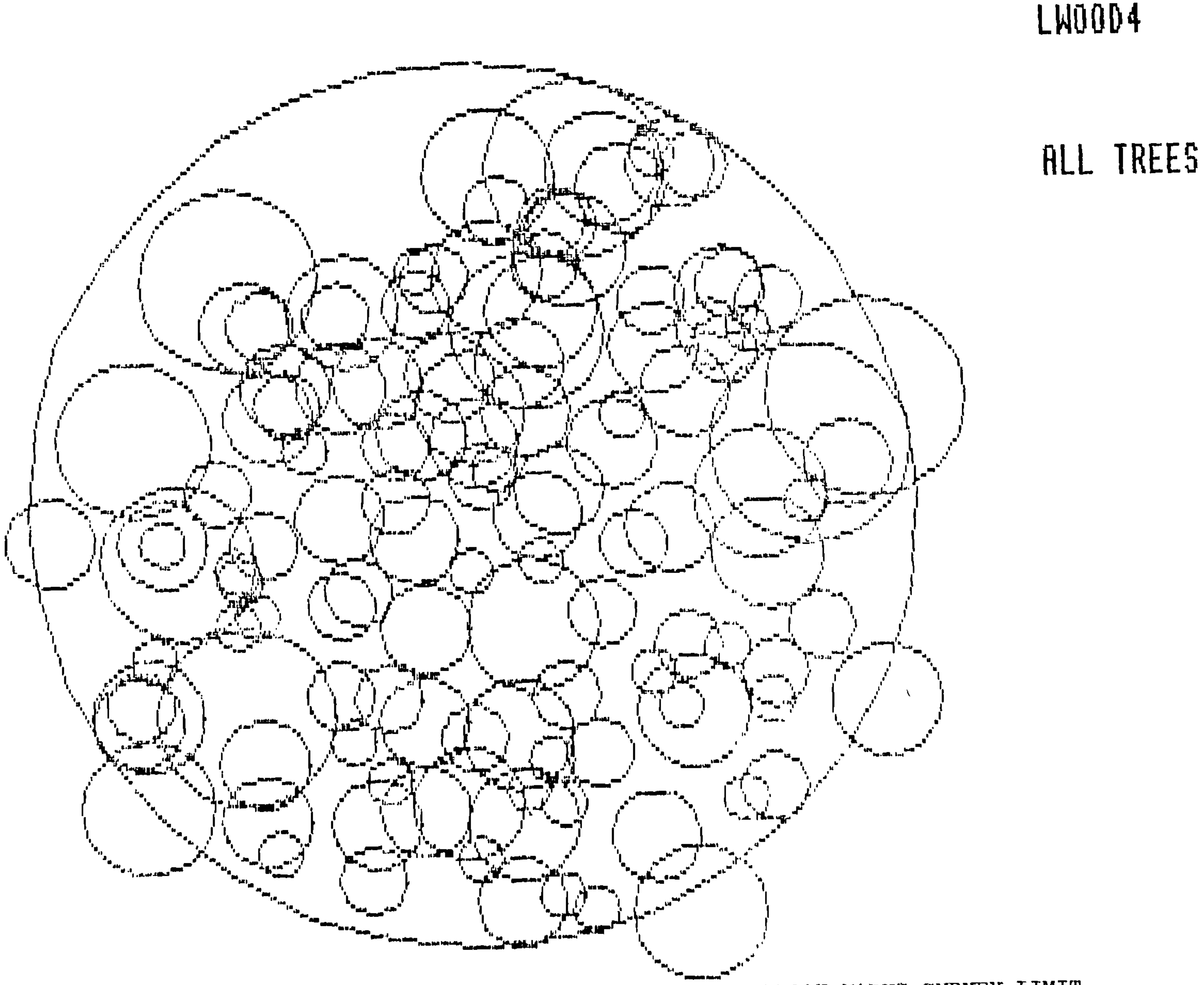


FIG. 5.12 DISTRIBUTION OF CANOPIES AT LITTLEWOOD 4. OUTER CIRCLE MARKS SURVEY LIMIT

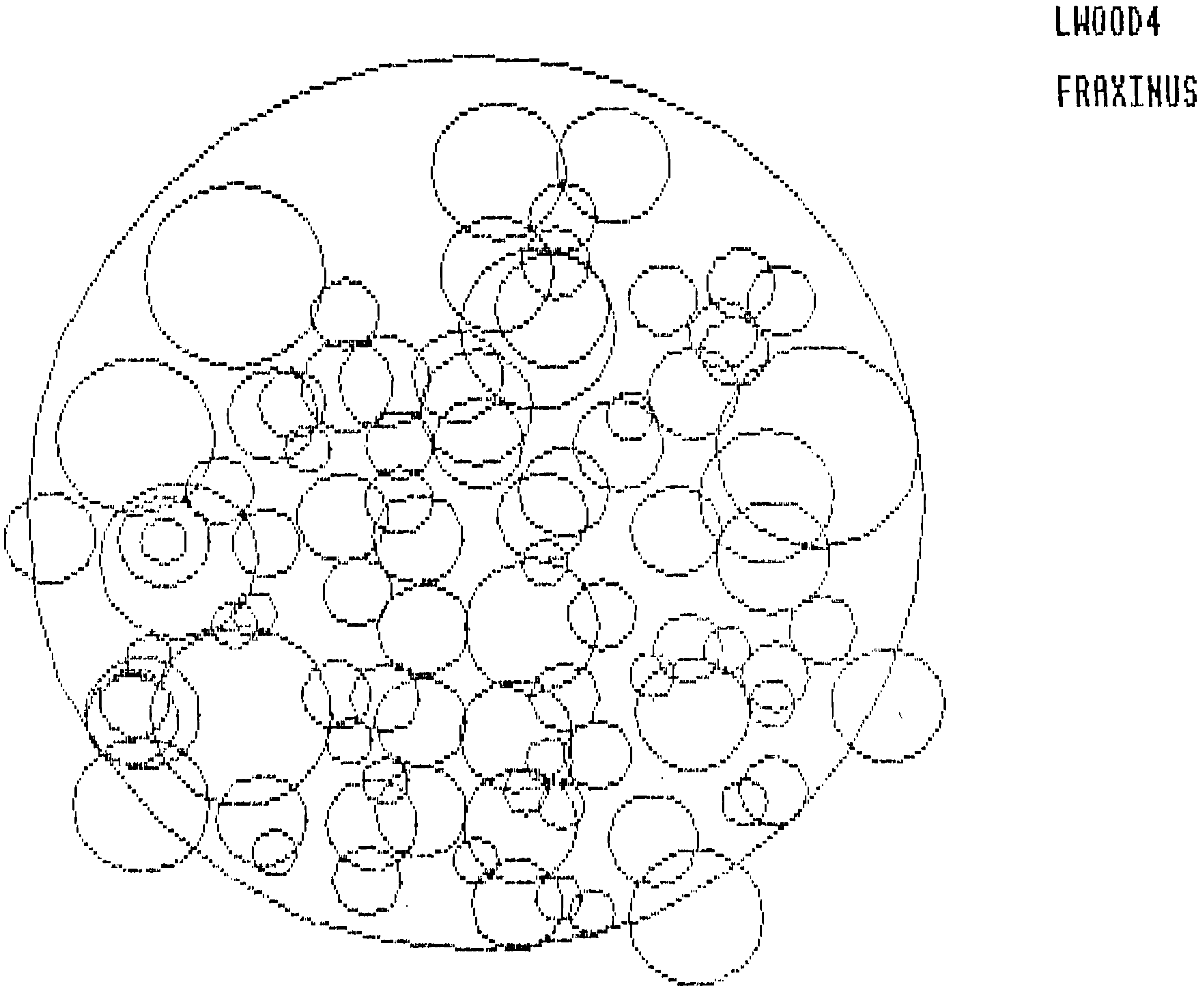


FIG. 5.13 DISTRIBUTION OF FRAXINUS EXCELSIOR CANOPIES AT LITTLEWOOD 4. OUTER CIRCLE MARKS SURVEY LIMIT

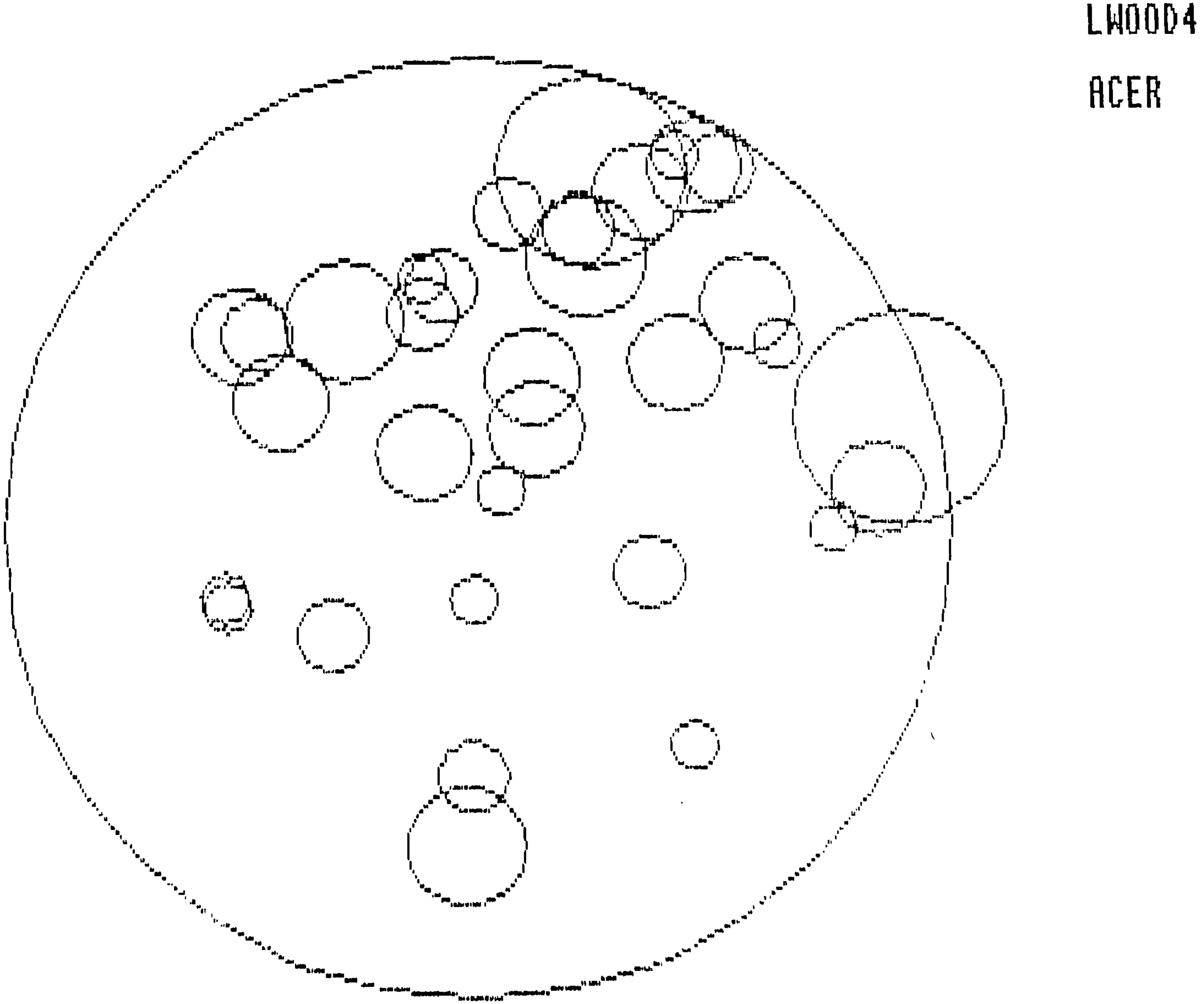


FIG. 5.14 DISTRIBUTION OF ACER PSEUDOPLATANUS CANOPIES AT LITTLEWOOD 4.

OUTER CIRCLE MARKS SURVEY LIMIT

recorded from the quadrat and yet their pollen was almost as abundant as that of F. excelsior. F. excelsior was shown to be a poor pollen producer by Andersen (1973) and Bradshaw (1981a), but even when the R-rel weighting factor was applied, the representation of Fraxinus was well below that of its canopy proportion. It may be that 1983 was a poor flowering year for Fraxinus, or it could be that these young trees were expending so much energy in racing upwards to the canopy, that they were not capable of flowering profusely. Certainly, these trees all had straight, thin trunks and a relatively small, lax canopy. This would support the argument that the energies of these trees have been channelled into upwards growth, rather than canopy development and flowering. This would be supported further by the lack of ash keys in the macrofossil sample.

The nearest individuals of Quercus or Betula to this quadrat were 50 to 70 m away. Over this distance the pollen influx had fallen from 1600 to 42 grains cm^2 y^{-1}, for Quercus, and from 2200 to 70 grains cm^2 y^{-1}, for Betula. This gives some indication of the degree of reduction in influx that might be expected with increasing distance from a pollen source. A further taxon to note is Tilia. This tree was not present in Littlewood, nor was it apparent in any of the local hedges. Therefore, it would seem that the pollen of this taxon found in the Littlewood samples was part of the regional pollen component. If an R-rel value weighting is applied to the Tilia total, the following transformation takes place. The two grains recorded represented 0.4% of the total pollen count, but the weighting, applied to the absolute data, suggests that Tilia represented 5%

of the local canopy. This serves to illustrate the danger of applying positive weightings to rare taxa.

The seed assemblage from this site had a concentration of 250 fruits per litre of soil, of which 54.4% were of arboreal taxa. Eight species were represented in the total; two were arboreal taxa, Betula (53.6%) and Sambucus (<1%). It will be remembered that no Betula tree was present within 50 m of this plot. It is clear, therefore, that the fruits are readily dispersed to more than 50 m from the parent tree.

The ground flora was made up of a dense carpet of Hyacinthoides non-scripta early in the year, and this was recorded at 41.8% of the vegetation cover. Deschampsia cespitosa and Milium effusum were the commonest of the grasses, which totalled 39.5% of the vegetation contacts. Dryopteris spp., the other major component of the ground flora, were present at 7.9%. The spores of Dryopteris accounted for 90% of the total pollen and spore influx to the site. If this taxon was excluded, and only the pollen total considered, then H. non-scripta (4% non-arboreal pollen), Gramineae (51% non-arboreal pollen) and Mercurialis (15% non-arboreal pollen) were the commonest pollen types. Of the 10 vegetation taxa recorded in the ground flora 8 were represented in the pollen record but only 3 in the propagules total. H. non-scripta pollen was again strongly underrepresented, as it was amongst the seeds where it only totalled 5.4% (non-arboreal seeds). Gramineae caryopses, cf. Milium, dominated the non-arboreal seed totals with 79%.

The bryophytes of this site were Eurynchium praelongum and

Hypnum cupressiforme.

Molluscs were poorly represented with a concentration of only 28 shells per litre of soil. Discus rotundatus, Cochlicopa lubrica, Carychium minimum, Aegopinella sp. and Arionidae were recorded.

5.8.3 Quercus Parkland

The third of the habitats at Littlewood was parkland, or an open woodland environment, in which selective felling had left only the largest trees (Figs. 5.15 - 5.17). In this area Betula pendula (27% of total canopy) became an important member of the Quercus robur-Corylus avellana association. Quercus robur was present at 36%, whilst C. avellana, Sambucus nigra and Acer pseudoplatanus shared the remaining 27% of the canopy. The ground flora was less diverse with a further increase in Dryopteris filix-mas, to 33.2% of the adjacent vegetation. Gramineae represented 37.4% of the ground cover and Hyacinthoides non-scripta was present at 11.7%, but the more sensitive woodland herbs were absent.

The pollen influx to this site was 12000 grains $cm^2 y^{-1}$ of which 55% was of arboreal taxa. 2300 grains were of Betula, representing 62.3% of the arboreal pollen sum. Quercus was represented by 11.5% of the arboreal pollen total. When these values had been weighted the resultant percentages were Betula 24.9% and Quercus 34.9%. These values were close to the measured canopy proportions, given above.

The concentration of propagules was the highest recorded at any of the sites with 2322 fruits counted from 0.4 litres of soil, giving a concentration of c. 5800 propagules per litre. Betula fruits represented 91.4% of this total. No acorns were found in the soil sample despite the presence of a mature specimen of Quercus robur within 5 m of the sampling site. The only other arboreal seeds were from Sambucus nigra and Salix sp.; these totalled 1.4% of the arboreal seed types.

All the five taxa of ground flora were represented in the pollen record. Gramineae was under-represented with 4.9% of the non-arboreal pollen sum, but, atypically, Hyacinthoides non-scripta was over-represented with 27%. This may have resulted from the direct input of an anther to the trap. Dryopteris was also over-represented with 60% of the non-arboreal pollen total.

The seed data included 3, out of the 5, species present in the ground flora survey. Gramineae (68% non-arboreal seeds) were heavily over-represented, Rubus (5%) and Hyacinthoides non-scripta (27%) made up the remainder of the non-arboreal seed total.

The bryophytes recorded from this plot included Rhytidiadelphus triquetrus and Fissidens taxifolius suggesting a lightly shaded or open environment.

The concentration of mollusc testa was 9 shells per litre. This was made up of Aegopinella nitidula and Euconulus fulvus, both catholic species, which show a slight preference for moist or shaded environments.

5.8.4 Quercus petraea-Betula pendula Woodlands

This woodland association is usually found on a neutral to acid substrate (Peterken, 1981), but at Anston Stones Wood, in the woodland margin between the arable fields and the steep valley sides there is such an association. The site was Anston 4 and as can be seen from Fig. 5.18 Quercus is the dominant tree producing 57% of the canopy. Sorbus aucuparia (9%) and Betula pendula (7%) were also present. The ground flora was characteristic of ancient woodland with Mercurialis perennis (47%), Hedera helix (32%) and Arum maculatum (<1%). Gramineae were present at 5% and Dryopteris at 3% of the adjacent vegetation.

The pollen influx to the site was low with 2617 grains cm^2 y^{-1}. Betula pollen made up 39% of the total pollen influx, which as a weighted arboreal percentage was, 16%. Quercus had a weighted arboreal percentage of 30% and Tilia, though not present in the plot, was 9.8% of the weighted arboreal total. The weighting has still left Betula over-represented and Quercus under-represented.

The concentration of propagules collected from this site was 1400 fruits per litre, comprising just three species: Betula (99.1%), Quercus (0.1%) and Rubus (0.8%)

The herbaceous pollen input to this site was 23% of the total; 47% of this was of Gramineae. Filicales were <1% and weeds of disturbed land formed 3.6% of the non-arboreal pollen sum. The latter would probably have been derived from adjacent fields. Woodland indicator species, e.g. Mercurialis, Hedera and Ligustrum, made up 30% of the non-arboreal pollen total. The

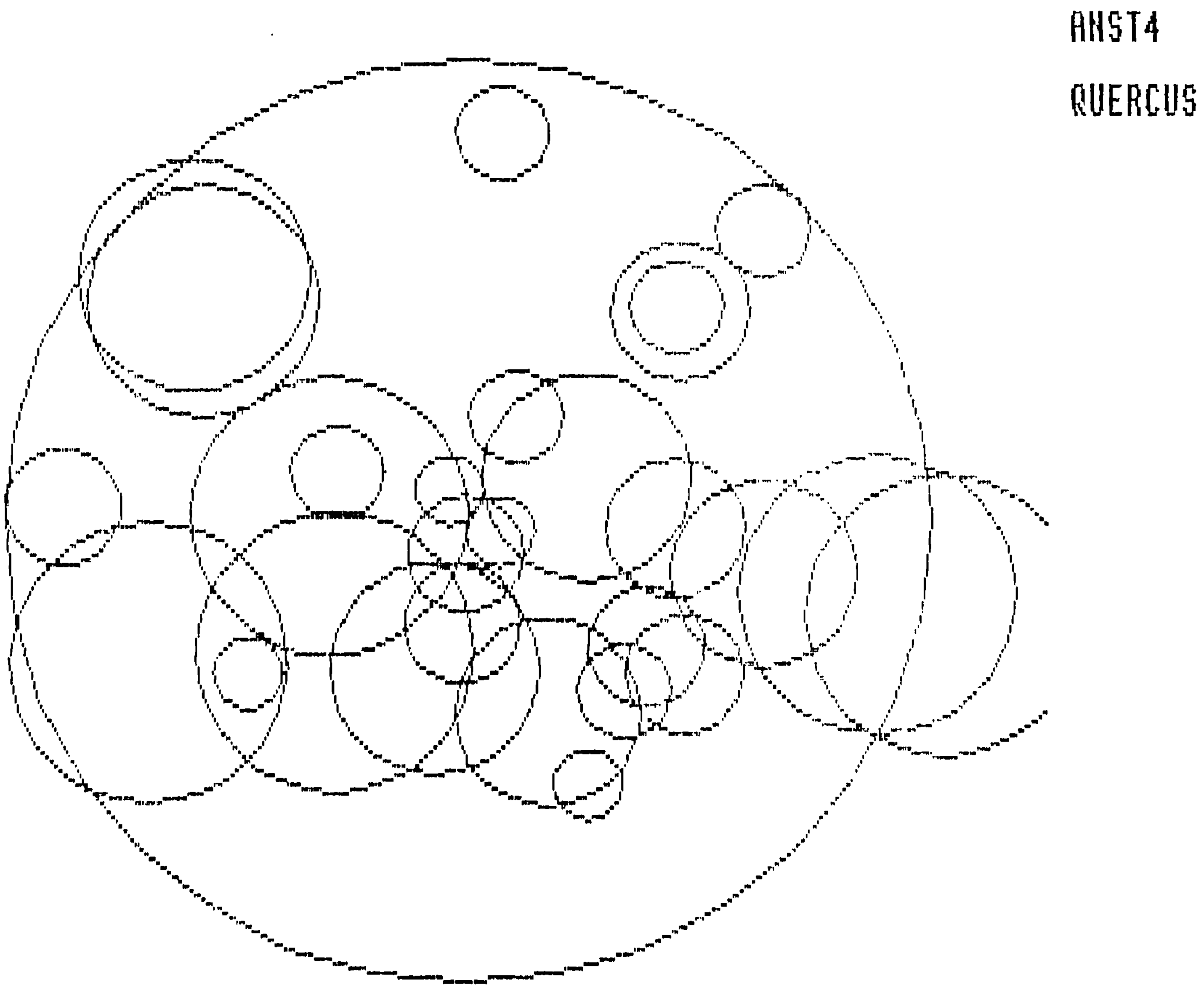


FIG. 5.18 DISTRIBUTION OF _QUERCUS_ SPP. AT ANSTON 4. OUTER CIRCLE MARKS SURVEY LIMIT

adjacent vegetation could have accounted for 96% of the pollen influx.

No bryophytes were recorded from this site.

The concentration of mollusc shells was 30 per litre of soil, of which none was strongly characteristic of a woodland assemblage. *Punctum pygmaeum* and *Vallonia costata* were both present. Particularly the latter is associated with open ground habitats. This might be a reflection of the very open canopy of this site, or the proximity (40 m) of arable fields.

5.9 MODERN ANALOGUE DATA FROM *TILIA* WOODLANDS

5.9.1 *Tilia*-*Corylus* Woodlands

In this association, found at Anston (1 - 3) and Kingswood (2), the dominant tree is *Tilia cordata*, with *Ulmus glabra*, *Quercus* spp., *Betula pendula*, and occasionally *Fagus sylvatica* as accompanying species. In the sites surveyed the percentage canopy component of *T. cordata* ranged from 28% to 61%. Where this value fell below 50%, *F. sylvatica* was to be found as a co-dominant; this was the case at Anston 3 and Kingswood 2. *Betula* attained a maximum value of 3% in Kingswood 2 but was not recorded from Anston 1 and 3.

The pollen influx to these sites ranged from 2700 to 10200 grains cm^2 y^{-1}. At Anston 1 and 2 the proportion of *Tilia* pollen exceeded its proportion of canopy area. This is in marked contrast to the value for Anston 3 where, despite a canopy area of 40.6%, the proportion of pollen attributable to this species was only 8.5% of the weighted arboreal pollen. These data are diplayed in Fig. 5.2.

SITE	% CANOPY	%WEIGHTED POLLEN	INFLUX	DISTANCE M
ANSTON 1	61.1	78.5	1402	0
ANSTON 2	51.3	79.7	1888	0
ANSTON 3	40.6	8.5	56	2
K'WOOD 2	28.5	25.3	191	5
K'WOOD 5	4.0	0.0	274	15
ANSTON 4	0.0	9.8	25	50

Table 5.2: Data relating to the representation of *Tilia cordata*.

As can be seen from these data the two sites Anston 1 and 2 had a vastly increased deposition compared to that from Anston 3. That the influx rates should be so different, for relatively similar canopy compositions, demonstrated that the high values of *Tilia* might be due to the direct input of anthers to the pollen traps. Figs. 5.19 - 5.21 show that the *Tilia* trees overhung the traps at Anston 1 and 2, but that the canopy stopped just short of the trap at Anston 3. Anthers of *Tilia* were recorded from the pollen traps at Anston 1 and 2 and also from Kingswood 1 and 4. It would seem highly likely that this was the cause of the apparent over-representation of this taxon in these plots. The data presented in Table 5.1 serve to illustrate the rapid decline in *Tilia* representation in the airborne pollen component with increasing distance from the pollen source.

At Anston 1 where there was no *Betula* growing within the

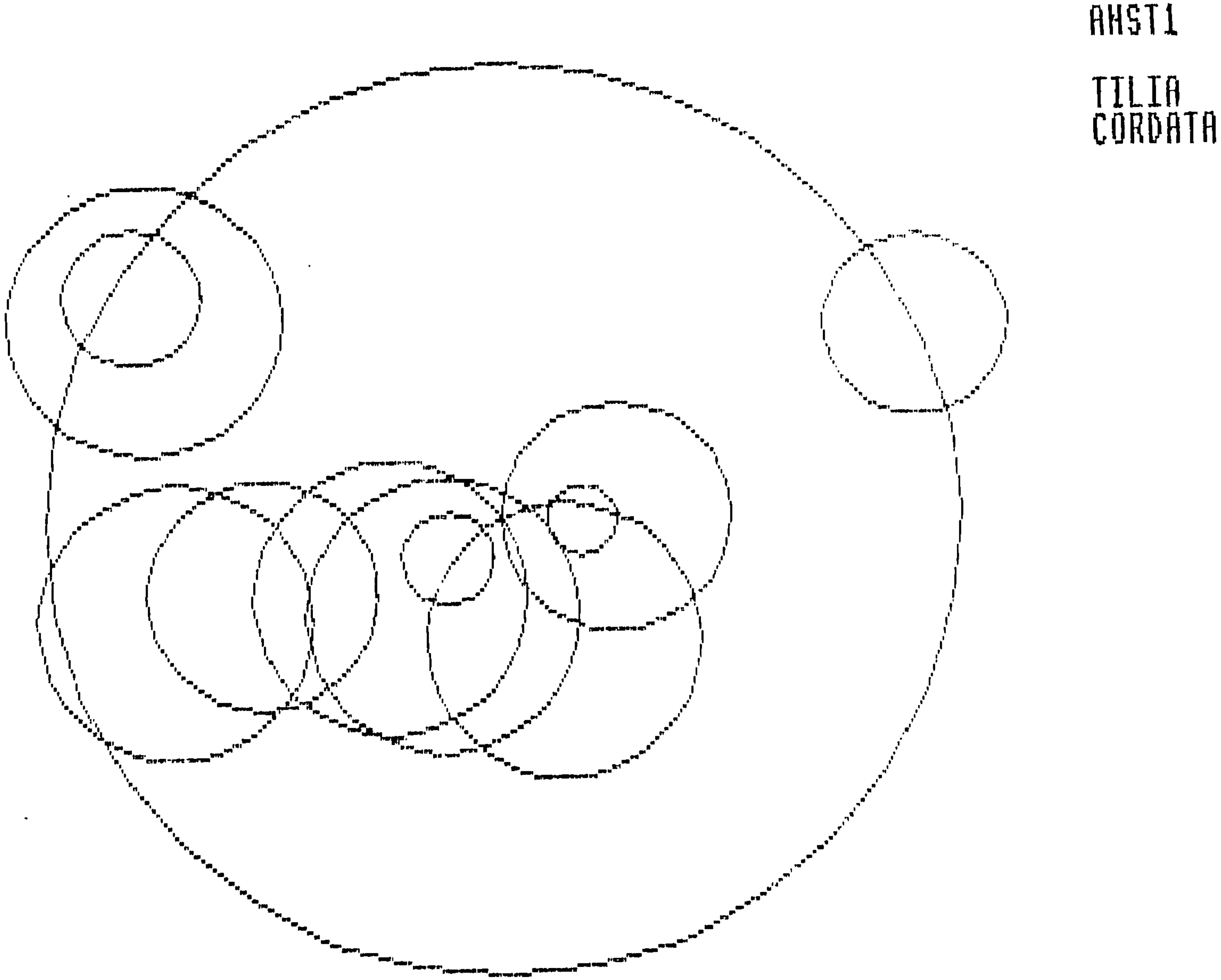


FIG. 5.19 DISTRIBUTION OF TILIA CORDATA CANOPIES AT ANSTON 1. OUTER CIRCLE MARKS SURVEY LIMIT

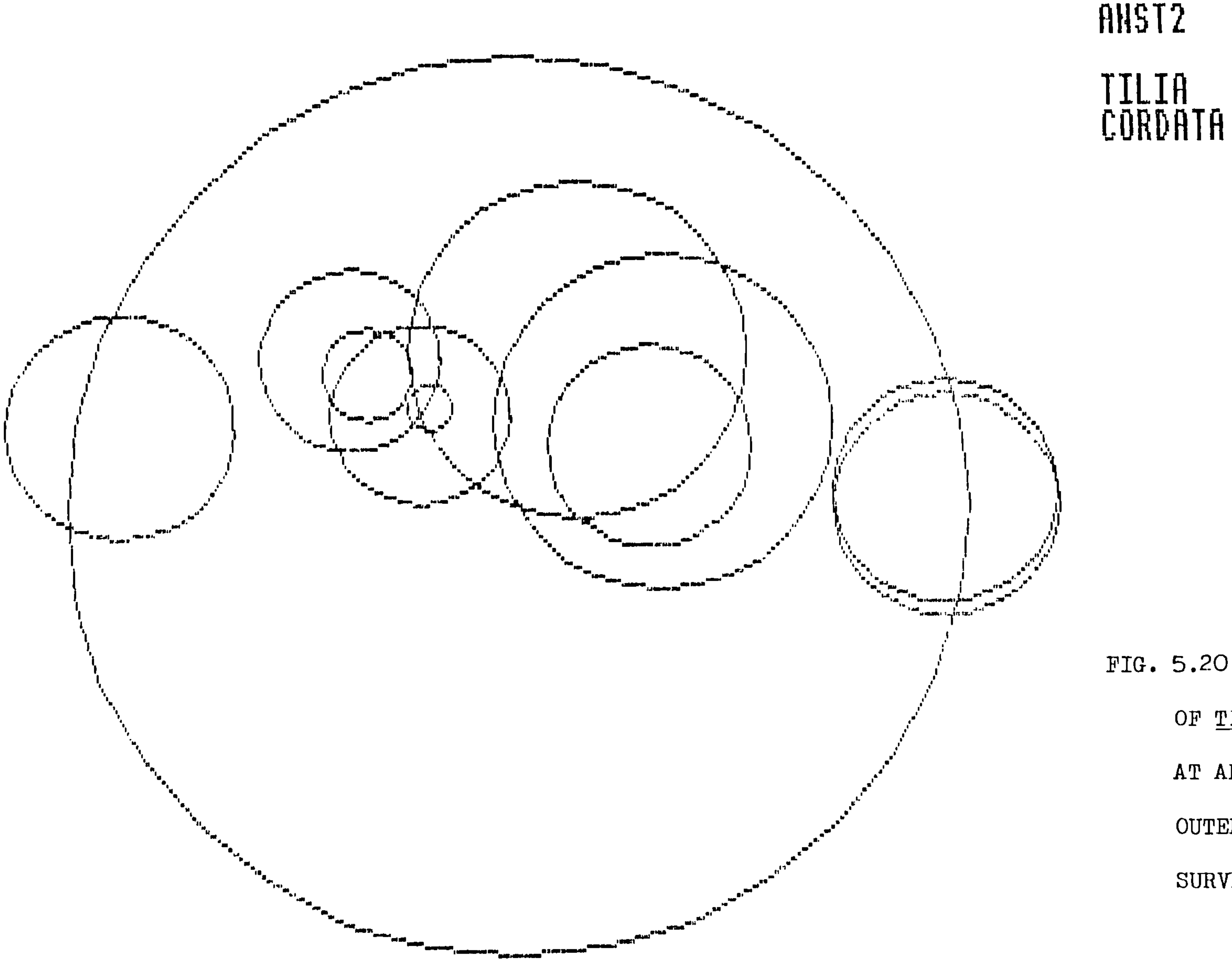


FIG. 5.20 DISTRIBUTION OF _TILIA CORDATA_ AT ANSTON 2. OUTER CIRCLE MARKS SURVEY LIMIT

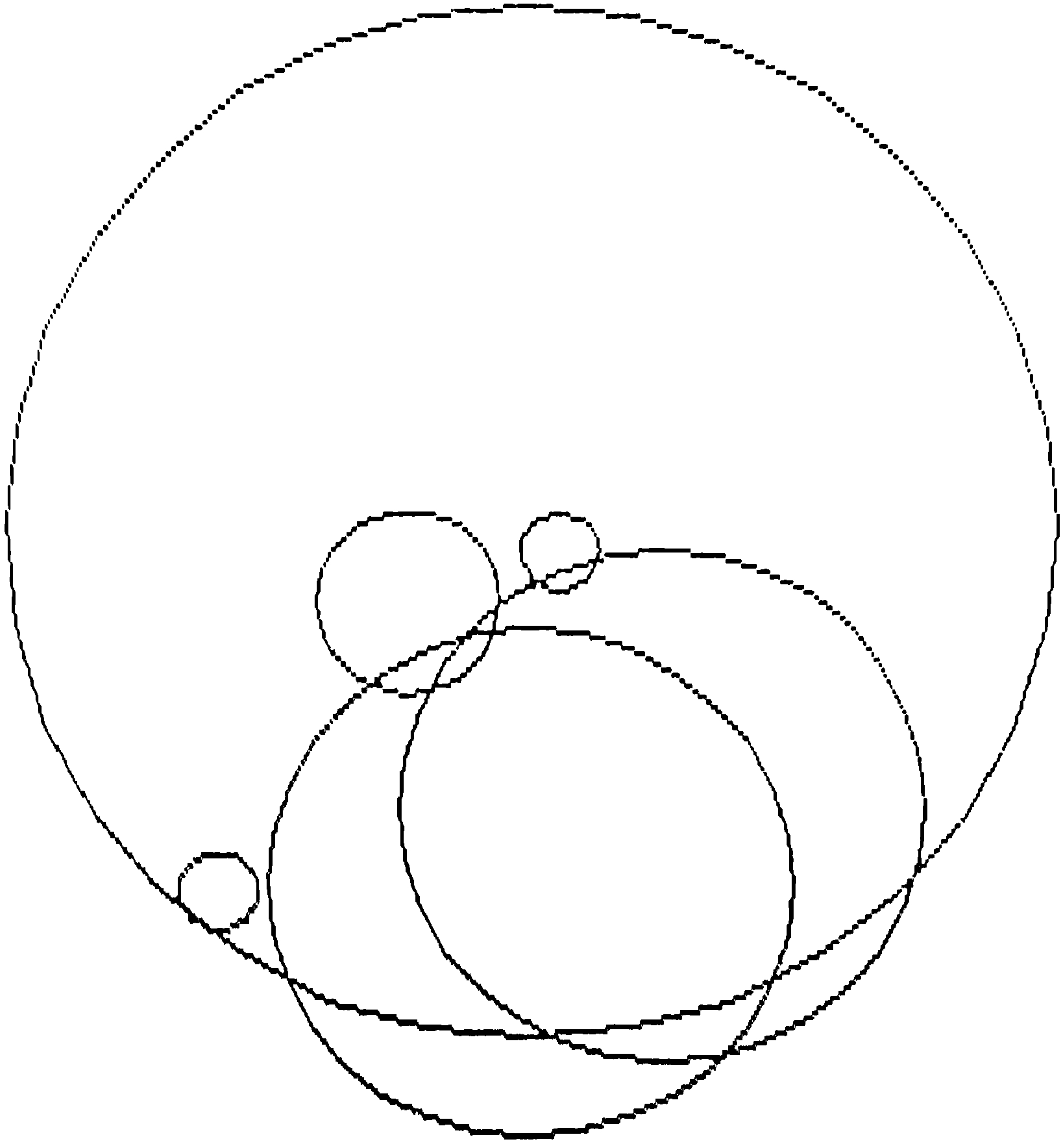


FIG. 5.21 DISTRIBUTION OF *TILIA CORDATA* CANOPIES AT ANSTON 3. OUTER CIRCLE MARKS SURVEY LIMIT.

quadrat there was an influx of 1838 grains cm^2 y^{-1}; a similar value of 1157 grains cm^2 y^{-1} was obtained from Anston 2. At Anston 3 277 grains cm^2 y(-1), representing 1.6% of the weighted arboreal pollen component, were caught from a site, where again there was no *Betula* in the quadrat. This site was situated on the edge of a beech hangar, on the opposite side of the valley from the other sites. No *Betula* was observed growing on this, the west side of the valley, and so the pollen must have travelled over 100 m to be caught in the trap at this site. This is perhaps a lower representation than might be expected from such an efficiently dispersed grain as *Betula*. The nearest pollen source lay to the east, and so the *Betula* pollen would have to have been carried against the prevailing wind.

Fagus sylvatica, though a dominant tree on the western valley side, contributed little pollen to the local pollen rain. At Anston 3, where large *F. sylvatica* grow on three sides of the sample point (Fig. 5.22), the influx of this species was only 395 grains cm^2 y^{-1}. Through weighting this representation was increased to 35.7% of the arboreal pollen component. *Acer pseudoplatanus* was another under-represented species. This finding agreed with the results obtained by Bradshaw and Webb (1985). They suggested that the entomophilous nature of this tree accounted for the low concentration of *Acer* pollen found from moss polsters collected in *Acer*-rich forests in America. An exception to this rule was provided by Anston 3 where the weighted pollen percentage for *Acer* was 27.5% compared with a presence in the canopy of 9.5%.

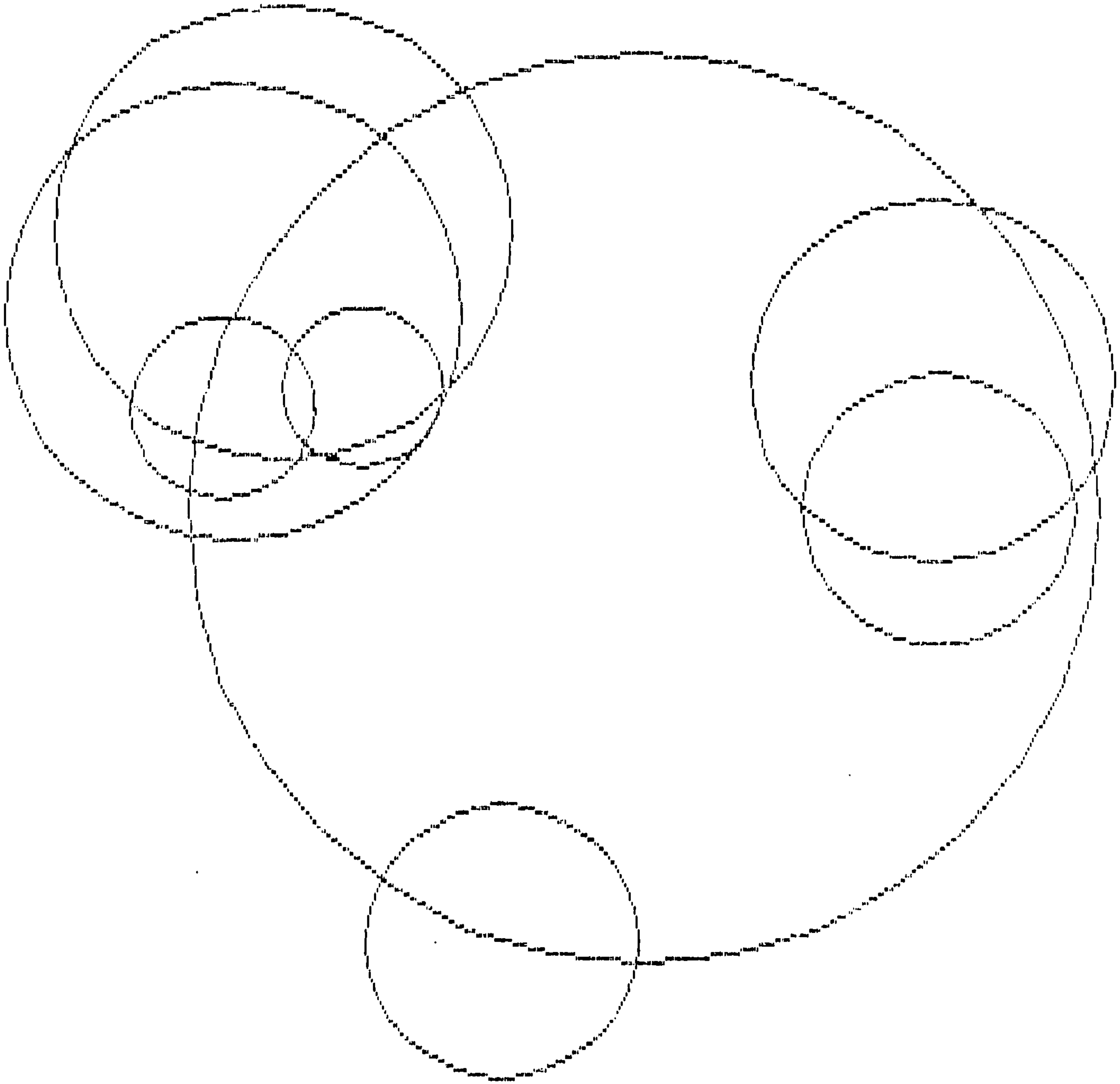


FIG. 5.22 DISTRIBUTION OF *FAGUS SYLVATICA* AT ANSTON 3. OUTER CIRCLE MARKS SURVEY LIMIT

The concentration of propagules at these sites ranged from 92 to 280 fruits per litre of sediment and the pattern of over-representation by Betula was repeated in all these samples. At Anston 1 where there was no Betula 84 fruits were recovered from 0.8 litres of soil. This represented 73% of the arboreal seed input. Tilia, which dominated the canopy and overhung the sample plot, contributed the remaining 27%. At Anston 2 there was a similar result. Betula, which formed 1.1% of the canopy, contributed 59.1% of the arboreal fruits. Again the remainder (40.9%) were Tilia fruits. On the opposite side of the valley, at Anston 3, fruits of Acer pseudoplatanus (41%) were the commonest, followed by Tilia with 24% and Fagus 7.5%. Even though no Betula tree was observed on this side of the valley 11 Betula fruits per litre of soil (13%) were recorded from this sample.

It would appear that the heavy seeds of forest trees such as Fagus sylvatica and Quercus spp. were poorly dispersed. Even the fruits which have large wings, such as Acer and Tilia, did not travel far from the point of release. However, the light winged seeds of Betula may be carried for considerable distances. This may also be true of Ulmus, although none was found. The absence of Ulmus propagules may have been the result of damage inflicted on these trees by Dutch-Elm disease.

The herb flora within the woodland was better represented by the pollen than by the propagules. The only fruits of herbaceous plants to have been derived from outside the quadrats were: Potentilla sp., Cirsium sp. and Chenopodium sp., all of which could have been bird-sown. The number of non-arboreal seeds in these samples ranged from 0 to 13, which was insufficient for a statistical comparison. However, the samples provided an assemblage with a strong woodland character through indicator species, e.g. Mercurialis perennis, Circaea lutetiana and Viola sp. (woodland type).

The pollen data gave a more complete record of the species present at each site. In each case over 50% of the species present in the ground flora were represented in the pollen data. This contrasts with the seed data in which there were less than 50% of the adjacent flora represented in the propagule record. There was considerable background 'noise' in the pollen data set; of the 8 local taxa in the ground flora at Kingswood 2, 5 were represented in the pollen data. However, there were another 22 herb taxa present in the data set, which were not present in the local vegetation. This would confound the interpretation of the herb pollen data at this site. For a comparison of the noise in the pollen and propagule data sets see Figs. 5.7 and 5.9.

Gramineae were over-represented in these sites with values from 48% to 61%, which did not reflect its actual presence in the vegetation of 0% to 1.6%. As a consequence of this the percentages of the other taxa were depressed. Mercurialis was consistently under-represented. Although the most abundant herb in these quadrats it did not exceed 15% of the non-arboreal pollen sum. At Anston 2, where it was recorded at 47% of the ground flora, no Mercurialis pollen was recorded from the trap.

The proportion of the adjacent vegetation, with some degree of representation in the pollen data, was 42% to 86%.

The bryophytes recorded from these sites were Amblystegium *varium*, *Eurynchium praelongum*, *Mnium hornum*, *Plagiomnium undulatum*, *Climacium dendroides* and *Solenostoma* sp.. This is an assemblage typical of mature woodlands on basic soils.

The concentration of mollusc testae in these samples ranged from 10 to 103 per litre of soil. *Acanthinula aculeata*, *Acicula fusca* and, at Kingswood, *Ena obscura* were present in these samples. All of these are species strongly associated with ancient woodland habitats (Paul, 1975). Others, though less specific woodland taxa, present were: *Discus rotundatus*, *Aegopinella nitidula* and *Vitrea crystallina*. Numerically the catholic species (80%) were found to outnumber the woodland indicator species (20%).

5.9.2 *Tilia-Taxus* Woodlands

Three woodland stands were grouped into this unit; all were in one section of the Kingswood, plots 1, 4 and 5. These woodlands were quite open in character, despite the presence of dense shade trees such as *Tilia cordata* and *Taxus baccata*. The rather open canopy may have been the result of windblow. Several large *T. baccata* were noted as having been blown down, revealing a widespread but shallow root formation.

At plots 1 and 5 *Tilia cordata* was the dominant tree (55% to 83% canopy area) whereas at Kingswood 5 there was only one *T. cordata*, forming 4% of the canopy. *Quercus petraea* (32%) was an important tree at this site, but the dominant tree was *Taxus baccata* with 48% of the canopy area. *T. baccata* will grow as a relatively small shrub in the understorey of a woodland, but if growing in an open woodland it will grow into a sizeable tree.

This was well illustrated by the canopy structure at Kingswood 1 where *Tilia cordata* formed a stand in the centre of the sample area. Beneath the *T. cordata* were small *T. baccata*. Where there was no overhanging *T. cordata* the *T. baccata* were considerably larger (Fig. 5.23). A similar pattern was found at Kingswood 5, where *Quercus petraea* was the shading tree (Fig. 5.24).

The pollen influx to these sites ranged from 3000 grains cm^2 y^{-1} at Kingswood 1, to 14500 at Kingswood 5. Of this total 71% to 83% was of arboreal pollen. The pollen influx to plot 1 was very low, especially in view of the fact that 2017 of the 2979 grains were contributed by *Tilia*; of the remaining 962 grains, *Betula* contributed 138 and Gramineae 188. Despite *Taxus baccata* being an abundant tree in this plot only 26 grains cm^2 y^{-1} of this taxon were deposited in the trap. Perhaps the overhanging branches of *Tilia cordata* were not only causing *T. cordata* to be over-represented, through a direct input of pollen. The sticky bark and foliage of this tree may have been filtering pollen out of the air, and so reducing the input of pollen to the trap. A mechanism of pollen interception similar to this was suggested by Tauber (1977). At Kingswood 5, where there were no overhanging branches the influx was much higher at 14500 grains cm^2 y^{-1}. This rate lies within the range of influx values for woodland pollen rain as measured by M.B. Davis *et al.* (1973) and R.B. Davis *et al.* (1975).

At Kingswood 5, the *Tilia* pollen was reduced to 1.6%, or an influx of 274 grains cm^2 y^{-1}, despite the presence of a mature tree growing within 15 m of the sampling site. *Taxus*

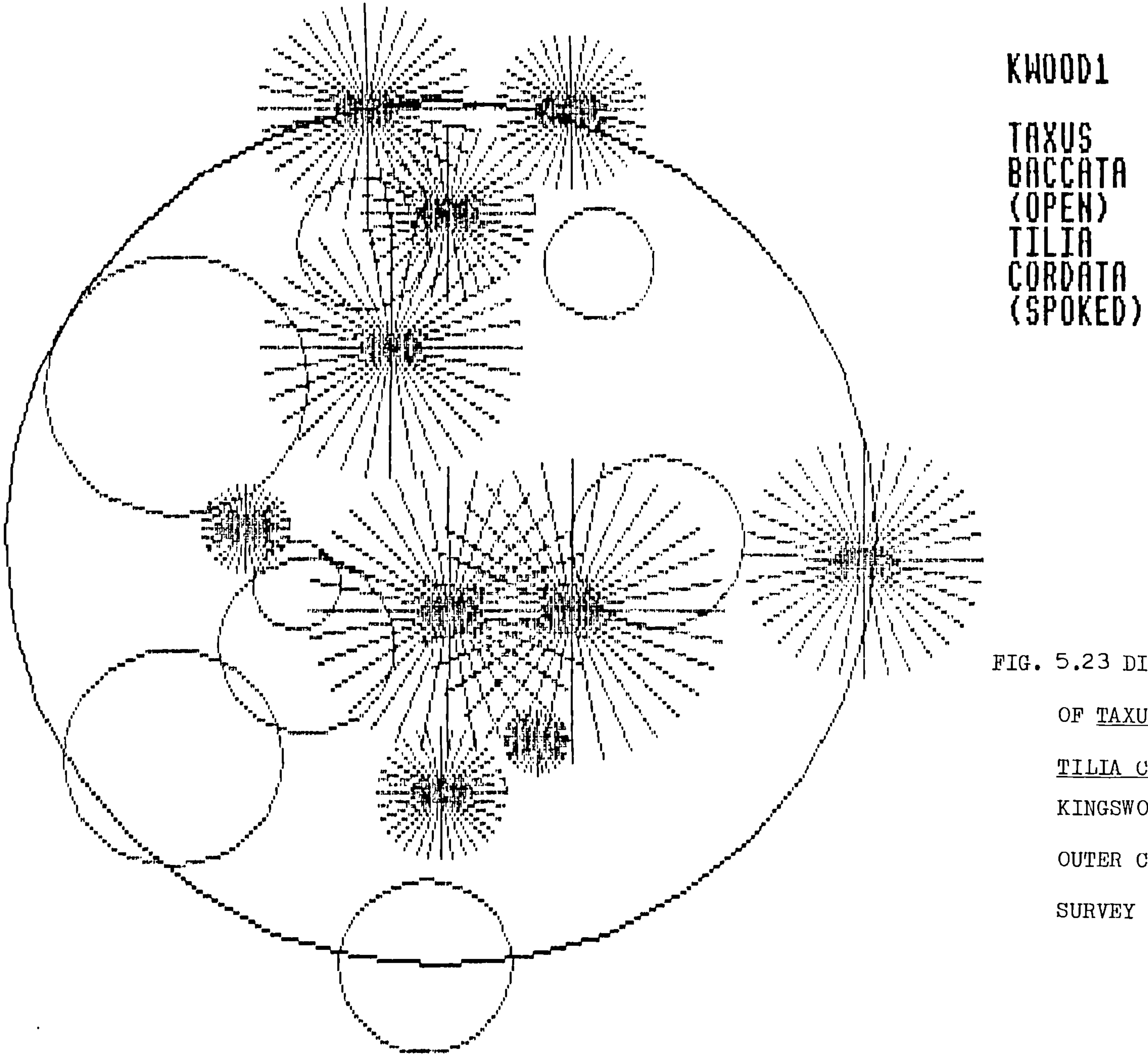


FIG. 5.23 DISTRIBUTION OF *TAXUS BACCATA* AND *TILIA CORDATA* AT KINGSWOOD 1. OUTER CIRCLE MARKS SURVEY LIMIT

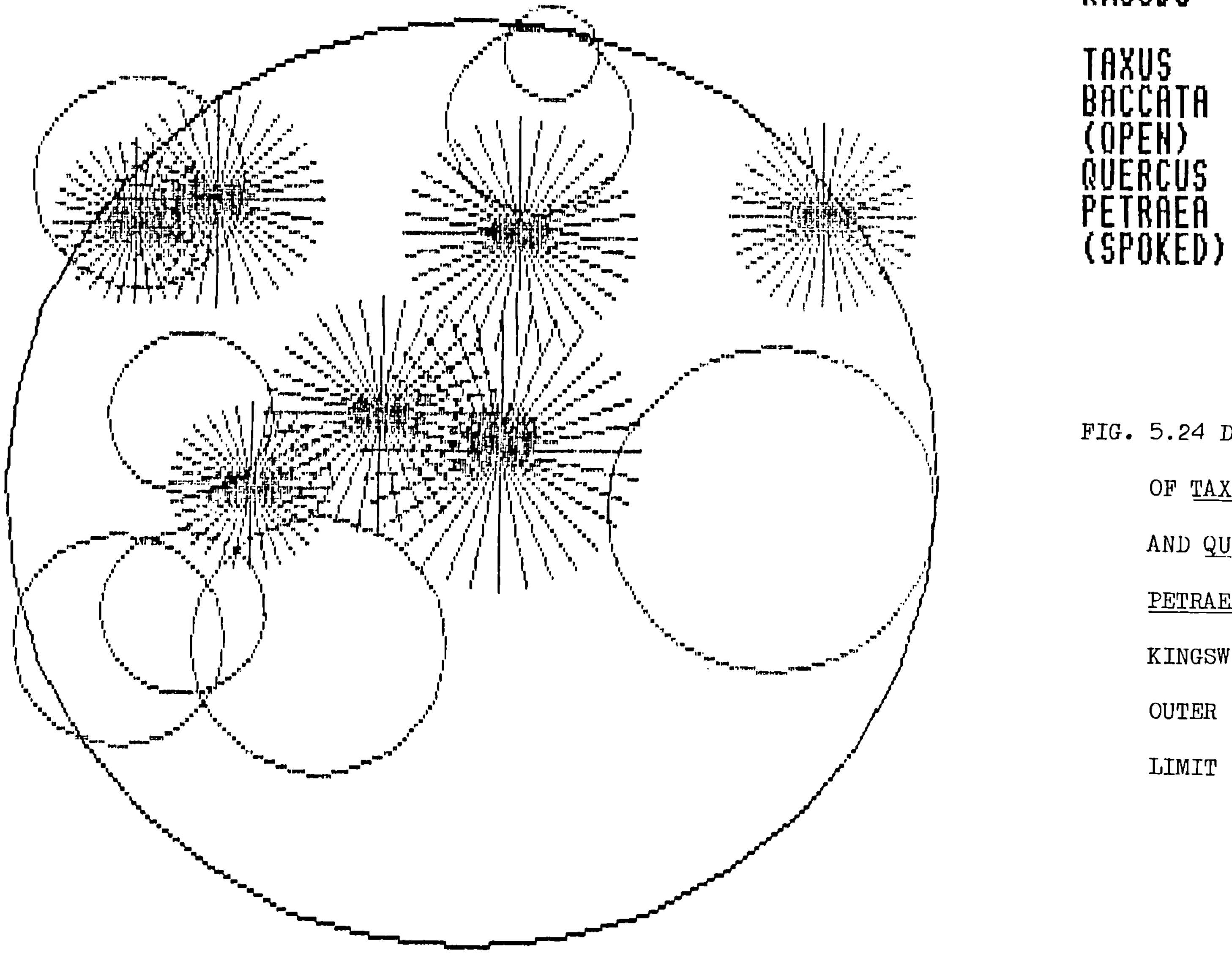


FIG. 5.24 DISTRIBUTION OF <u>TAXUS BACCATA</u> AND <u>QUERCUS PETRAEA</u> AT KINGSWOOD 5. OUTER CIRCLE MARKS LIMIT OF SURVEY

formed 37.3% of the arboreal input at this site, and Quercus accounted for 26.8%. This would be in accord with the suggestion that T. baccata flowered much more profusely when it was a member of the upper canopy rather than the understorey (Bradshaw, 1981a).

At plot 4 1846 grains cm^2 y^{-1} of Betula were deposited, this represented 43% of the arboreal input even though the percentage of Betula in the canopy at this plot was only 4% (600 m^2) and the nearest tree was 14 m from the sampling site. At Kingswood 5, where no Betula was recorded within the plot, the influx was 2980 grains cm^2 y^{-1}, greater than that of Quercus (2310) which overhung the pollen trap.

The concentration of fruits in these samples was 500 to 1200 fruits per litre of which Betula accounted for 87% to 96.5%. Tilia fruits were also present in all the samples, 12 occurring at plot 5, indicating that the winged Tilia fruits have some power of lateral dispersal.

The herb flora of these sites was species poor with Mercurialis perennis dominating the ground layer at Kingswood 1 and 4, and a mixture of Pteridium aquilinum and Mercurialis perennis at plot 5. The presence of P. aquilinum at this site suggests that the Quercus petraea canopy at this site allowed more light to reach the ground layer than was admitted by the Tilia cordata and Taxus baccata canopies of the other plots.

Gramineae were not recorded in the ground flora of any of these sites and yet 43% to 57% of the non-arboreal pollen was of this group. As with the other Tilia cordata woodlands the representation of the local ground flora was obscured by the extra-local and regional pollen input (Fig. 5.5). At Kingswood 5, only one of the three taxa present in the gound flora was represented in the pollen spectrum, but a further 11 non-arboreal pollen types not recorded in the adjacent vegetation were present in the pollen sum.

The propagules yielded highly specific environmental information with the presence of *Mercurialis perennis* as the most frequent non-arboreal seed. At Kingswood 4, the proximity of a nearby track was indicated by the presence of *Epilobium* sp. and *Cirsium* sp., both of which would be likely to grow in a disturbed woodland fringe.

The bryophytes from this group of sites were representative of a mature woodland, e.g. *Ctenidium molluscum*, *Rhizomnium pseudopunctatum*, *Hypnum cupressiforme*, *Mnium hornum*, *Fissidens taxifolius* ssp. *taxifolius*, *Climacium dendroides* and the liverwort, *Lophocolea bidentata*.

Mollusc testae were present in low concentrations, from 10 to 65 shells per litre of soil. The assemblages were characteristic of ancient woodlands with *Acanthinula aculeata* present in all the samples, and *Ena obscura* present in the sample from plot 4. Once again, the true indicator species were outnumbered by the catholic species, which accounted for 88% to 95% of the total.

5.10 MODERN ANALOGUE DATA FROM OPEN WATER HABITATS

The two open water sites of Brandesburton Gravel Pit and Leven canal did not have accompanying vegetation data, although a species list of the abundant plants at each site was made. As the surrounding vegetation was thoroughly disturbed, and the sites were selected for their aquatic habitat, a palynological study of the sediments was not carried out. The collected samples were analysed for propagules and molluscs. It was not possible to estimate the concentration of these in a way comparable with that used for the other sites because the sediments were so water laden.

Alnus was a common fruit in the Leven canal assemblage, presumably having drifted into the deposit after dropping from an alder tree. *Alnus* were present along the bank; the closest overhung the canal *c.* 10 m from the sampling point. *Sagittaria sagittifolia* was an abundant plant at this site, covering much of the bed of the canal, and yet only one fruit of it was recorded. *Potamogeton lucens*, *P. crispus* and *P. alpinus* have been recorded from Leven canal (Crackles, 1968). However, the sample analysed contained no fruits of this genus, despite having been collected from a site where *Potamogeton* was in evidence. *Hydrocotyle vulgaris* and *Menyanthes trifoliata* were both recorded from the sample, although they were not seen amongst the bankside vegetation. The fruits of both these species are buoyant and it may be that they had drifted into the deposit. *Ranunculus* sec *Batrachium* fruits (15%) may have been derived from the locally abundant *Ranunculus aquatilis* ssp. *fluitans*. The proportion of obligate aquatic seeds in this sample was 24%, with a further

31.3% made up of *Carex* fruits.

The sample from Brandesburton Gravel Pit was dominated by fruits of *Alisma plantago-aquatica* (35%). Other aquatic species included *Potamogeton praelongus* agg., *Typha* and *Ranunculus* sec *Batrachium*. The commonest submerged aquatic in the pool was *A. plantago-aquatica*, and *Typha* sp. was the most abundant of the emergent plants at Brandesburton. Although *Typha* formed a near continuous fringe around the pool only two fruits of this taxon were found in the sample. Obligate aquatic taxa formed 40% of the seed total and *Carex* spp. accounted for a further 8%.

The paucity of this flora, which did not have the diversity or the maturity of the association at Leven, was reflected in the diversity of the propagule assemblage. Seventeen propagule taxa were present in the sample from Brandesburton as compared with 40 fruit taxa from the Leven sample.

One factor which might account for this is the size of the respective water bodies. Leven Canal, which is 5 km long, covering 20 ha, provides a much larger catchment for seeds than the small *c.* (0.8 ha) pool at Brandesburton.

No bryophytes were recorded from the pool at Brandesburton. However, five species were identified in the sample from Leven Canal. These were: *Cratoneuron filicinum*, *Barbula* cf. *recurvirosta*, *Drepanocladus revolvens*, *Fissidens taxifolius* and *Hypnum cupressiforme*. All of these are species characteristic of base-rich aquatic and bankside environments.

The mollusc faunas were dominated by obligate aquatics at both sites. At Leven Canal *Pisidium* spp. contributed 66% of the shells in the sample and Oxyloma pfeifferi 22% of the total. The remaining 12% was made up of 9 species, all of which were obligate hygrophiles, e.g. Valvata macrostoma, Anisus leucostoma, Armiger crista, Planorbis carinatus and Planorbarius corneus.

The sample from Brandesburton contained 3 species, Planorbarius corneus (84%), Oxyloma pfeifferi (12%) and Armiger crista (4%). These species were all present at Leven Canal and the difference in species diversity may be a reflection of the relative age of the two sites as much as a difference in the habitats.

5.11 CONCLUSIONS DRAWN FROM THE STUDY OF MODERN ANALOGUE SITES

5.11.1 Representation of the Gramineae

Palynological studies are based on the premise that there is a significant relationship between the occurrence of a plant, and the proportion of pollen which that plant has contributed to the pollen sum. It is disturbing to find that Gramineae, one of the most important indicator taxa, appeared to fail to conform to this criterion in the present study. It can be seen from Fig. 5.25 that there was no apparent relationship between the number of Gramineae contacts along a transect and the Gramineae pollen influx to that site. To explain this one could question the validity of the survey method, but even on a strictly qualitative basis one would expect consistently more Gramineae pollen from a grassland than from a woodland containing little grass.

If the vegetation survey was not the principal source of error then perhaps the calculation of the influx rates was at fault. The technique of adding exotic pollen, as first suggested

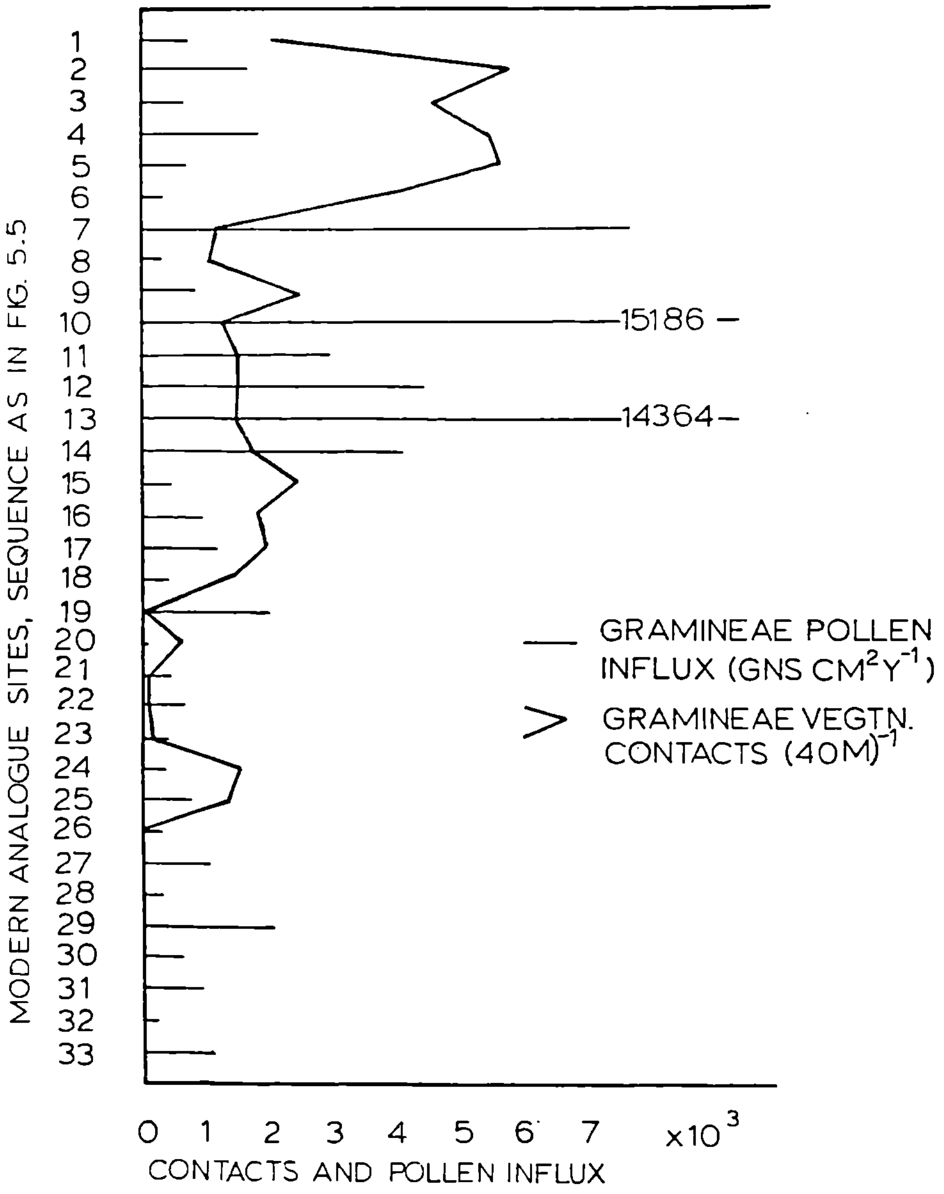


FIG. 5.25 : GRAMINEAE POLLEN INFLUX DATA COMPARED WITH THE DENSITY OF GRAMINEOUS VEGETATION AT THE MODERN ANALOGUE SITES.

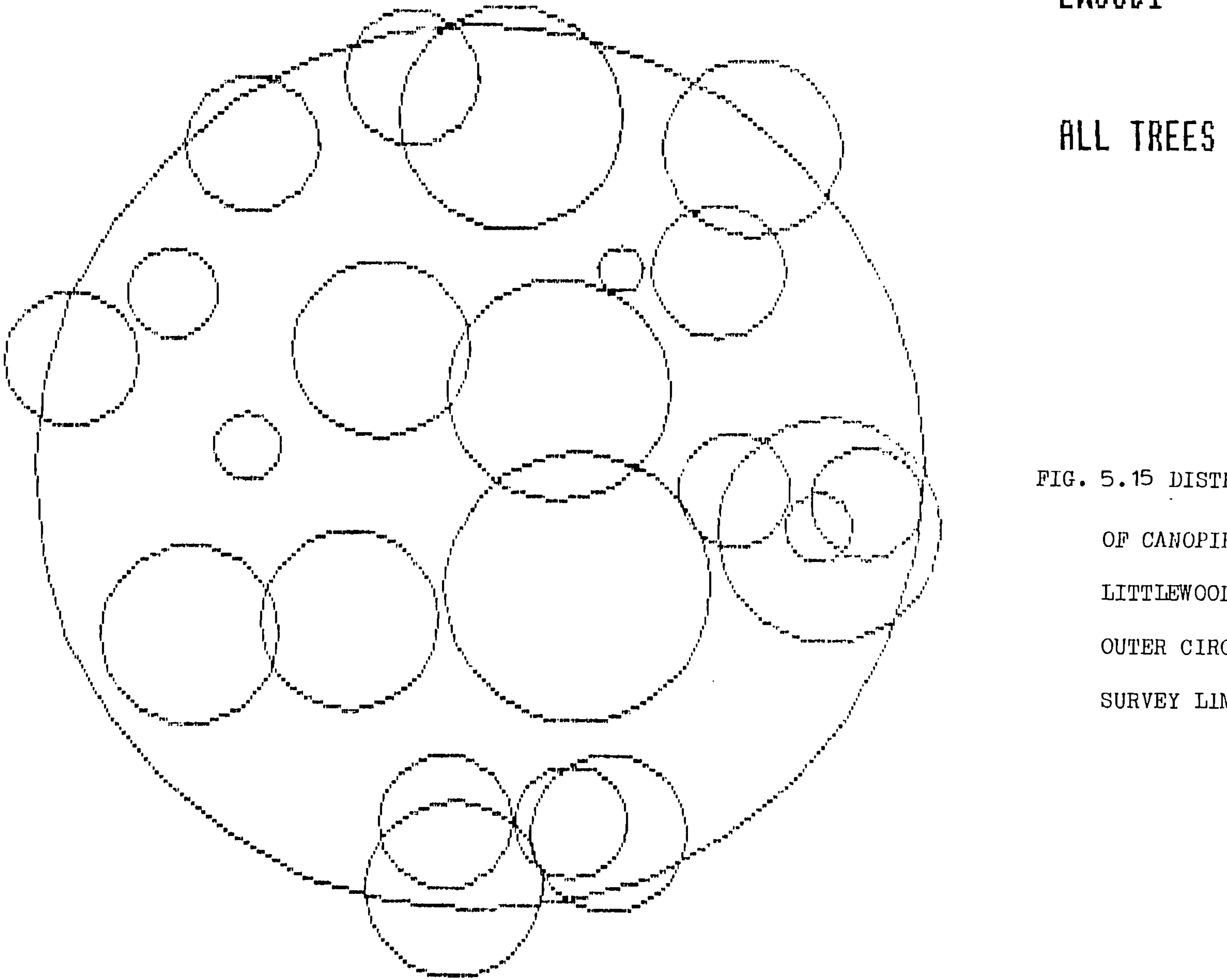


FIG. 5.15 DISTRIBUTION OF CANOPIES AT LITTLEWOOD 1. OUTER CIRCLE MARKS SURVEY LIMIT

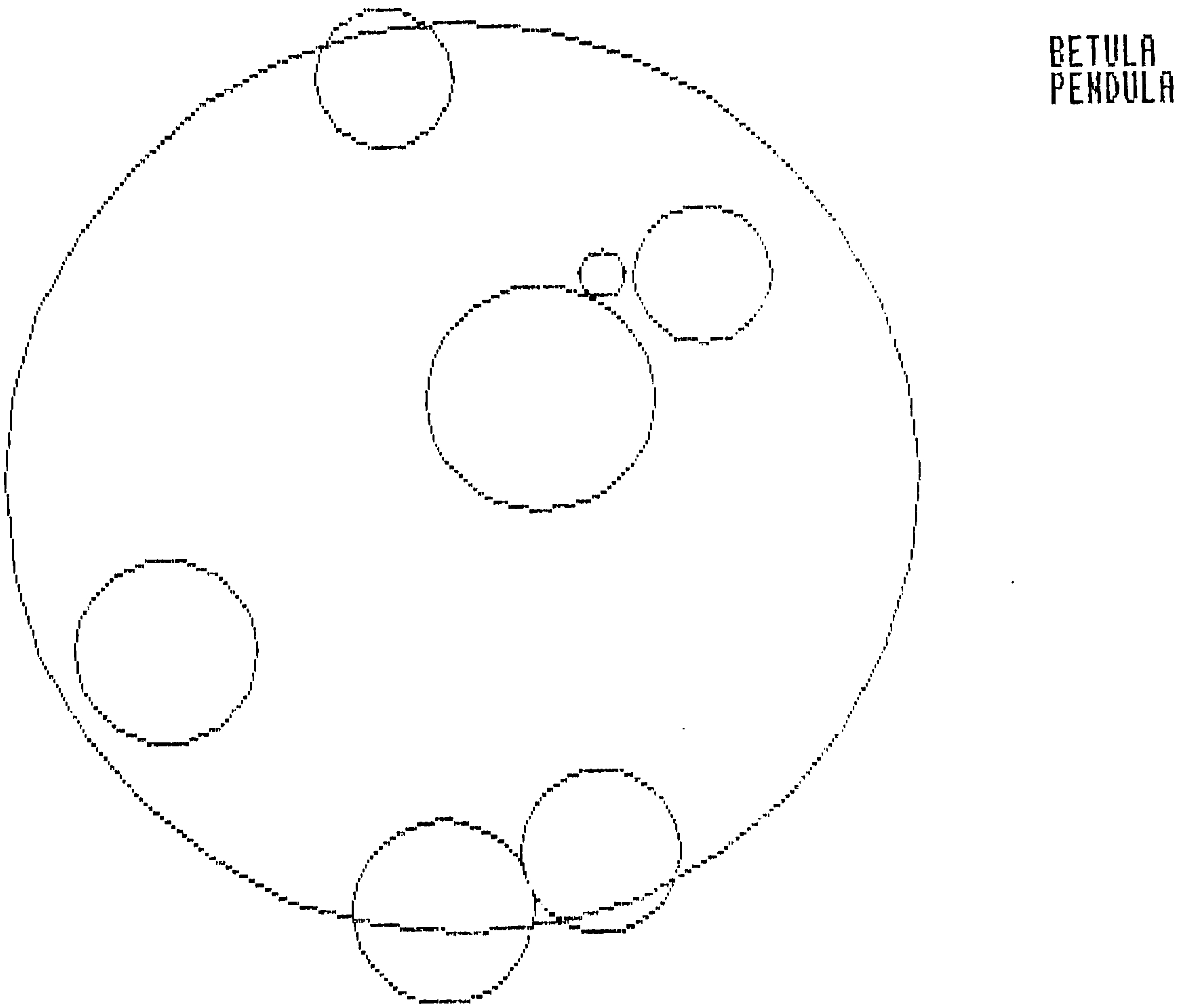


FIG. 5.16 DISTRIBUTION OF BETULA PENDULA CANOPIES AT LITTLEWOOD 1. OUTER CIRCLE MARKS SURVEY LIMIT

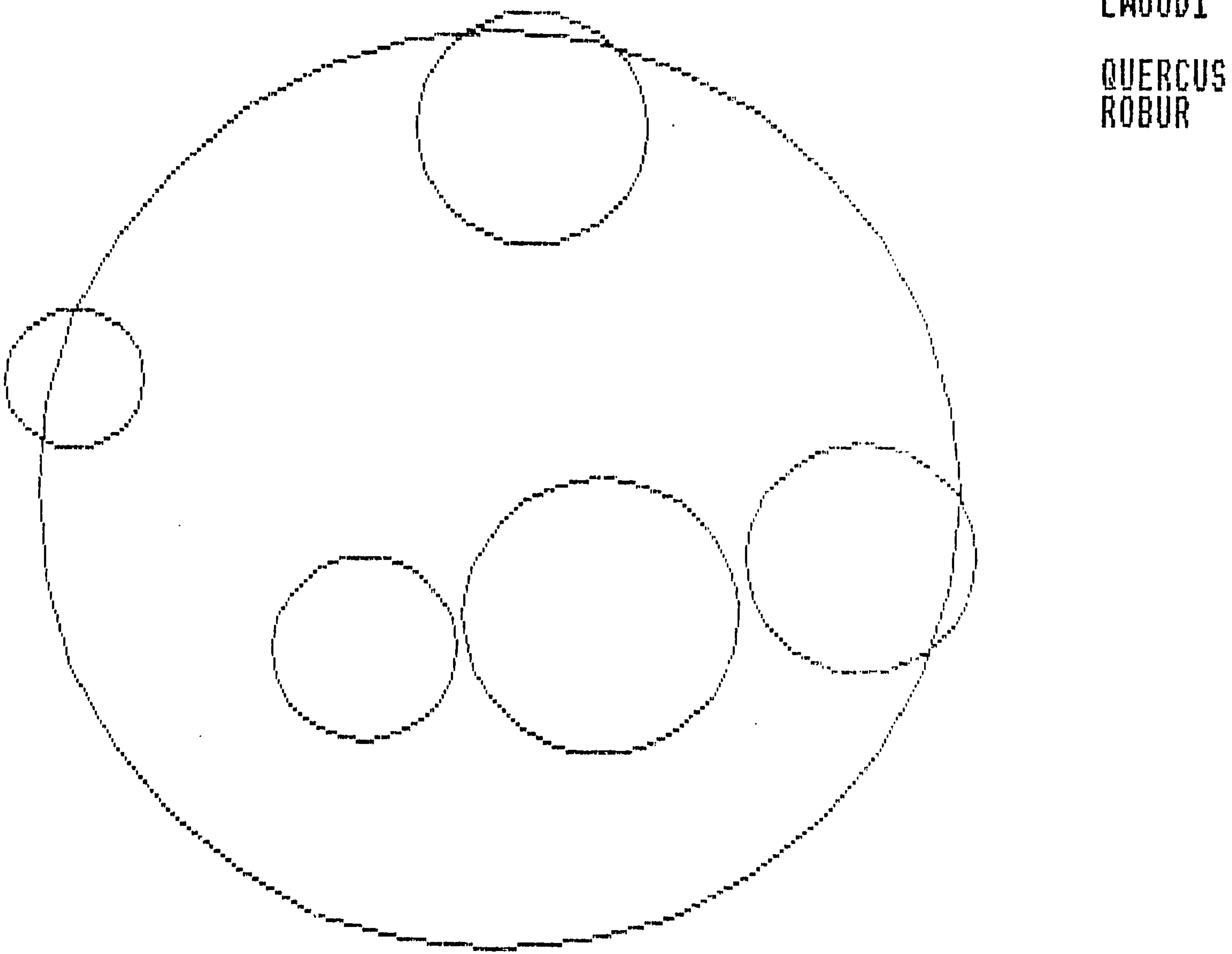


FIG. 5.17 DISTRIBUTION OF <u>QUERCUS ROBUR</u> AT LITTLEWOOD 1. OUTER CIRCLE MARKS SURVEY LIMIT

by Benninghoff (1962), and the use of Lycopodium tablets for influx calculations advocated by Stockmarr (1971), was tested and approved by Bonny (1972). It is possible that this technique is not ideal, but if there are errors they are at least likely to be consistent.

Perhaps the pollen traps were simply more efficient in the still air of the woodland floor, than on the windy slopes of the Yorkshire Wolds. If this were the case, the pollen trap at Fordon 7 would be expected to have a higher pollen influx than the traps set in open grassland, as it was sheltered in the lee of an ash copse. This trap did not have a particularly high influx and so perhaps another explanation might be sought.

Another influence which could have had a profound effect on pollen production and deposition was grazing. At Fordon Chalk Bank the sward is maintained by grazing rabbits and cattle. It is noticeable that the commonest plants of this association were Festuca spp., Helianthemum chamaecistus and Thymus praecox, all of which are capable of vegetative reproduction. If grazing was damaging the plants, and hence inhibiting flowering, or if flower heads were being grazed off, then the total pollen influx might be expected to be low. Some areas would be especially prone to such pressures, e.g. around rabbit holes, or in sheltered locations where cattle can graze out of the wind. Grazing may also prevent the secondary deposition of pollen. Pollen liberated from an anther may come to rest on leaves, until washed free by the rain. If these leaves are then eaten by cattle the pollen will pass through the gut of the animal before it is redeposited

(Carr, 1983). The redeposition may take place at some distance from the pollen source. The high pollen influx at Kiplingcotes Spring, which was an ungrazed grassland provided an indication of the capacity of a grassland for pollen production.

It would seem a reasonable hypothesis that grazing pressure was reducing the representation of Gramineae pollen from grasslands, but it does not explain the high Gramineae values obtained from the woodland sites.

This latter point is probably a reflection of man's disturbance of the landscape. Through forest clearance, agriculture and urbanisation, the regional pollen input will not reflect the surrounding forests, as it did in the early post-glacial. Instead it reflects the generally open landscape which man has created. Gramineae pollen would appear to be the major background component in modern pollen samples and unless the forest is large enough to provide its own regional component Gramineae will be an over-represented taxon.

5.11.2 Additional Summary Notes on Representation

Pinus pollen was a consistent component of the pollen influx at almost all sites although no individuals of Pinus were recorded within or in the vicinity of any sample area. It is apparent that the pollen of this species is extremely efficiently dispersed. However, it is not possible to obtain a 'background' influx level for a meaningful comparison with palaeoecological data as the past Pinus forestation might have borne no similarity to the present distribution of this species.

Another frequently over-represented taxon in both pollen and propagule diagrams was *Betula*. The rate of representational decrease with increasing seed-source distance was estimated. It was concluded that *Betula* growing within 50m of a sample site would be heavily represented in the propagule record of a fossil deposit. Beyond that limit the level of representation will fall close to a 'background' level.

The effect of shading on the pollen production of understorey taxa, e.g. *Taxus baccata*, was evident. Where there was reduced shade there was a marked increase in pollen production. However, increasing light also led to increased canopy size so that a significant positive relationship was observed between pollen production and the weighted cnopy area for most understorey and canopy dominant species.

5.11.3 The Relative Uses of Pollen and Macrofossils in Vegetational Reconstructions

The use of modern analogue studies to a palaeoecologist is in providing a guide to the proportions, and combinations, of taxa which may be expected from given habitats.

In this study it has been noted that pollen may yield a 'noisy' data set, making it difficult to separate the local from the regional pollen component. Webb *et al*. (1978) stated that what was thought of as noise in trying to reconstruct climatic change, or a broad regional vegetation pattern, may be exactly the detail necessary to detect small-scale, local vegetation changes.

One way to attempt to resolve this difficulty is to undertake the study of macrofossils. These should give a clear indication of the changes in the local habitat, thus helping to define which taxa are likely to be of local or regional importance. With the notable exception of Betula, the general assumption, that the fruits will accurately represent the local vegetation, was supported by this study. The concentration of Betula fruits would seem to be a better measure of the distance of the propagule's source, rather than the abundance of the tree.

The fine resolution of identification possible when studying fruits and seeds resulted in a far more detailed environmental image than that obtained through pollen analysis. This was especially noticeable in the grassland and fen sites. In these environments the identification of plants to a specific level is particularly important, as members of the same genus may have entirely different ecological requirements. Some key grassland taxa are identifiable through pollen analysis, but in many ways palynology is a technique better suited to analysing woodland environments. The arboreal species are generally prolific pollen producers and have readily identifiable pollen. Furthermore, the identification of the main canopy components would define the environment without the necessity for identifying herb taxa to species.

The woodland propagule assemblages gave enough information to define a broad habitat type, but the representation of many of the woodland taxa was so poor that this technique was best used to supplement the palynological study rather than to replace it.

The usefulness of molluscs for a palaeoecological reconstruction is limited by their lack of specificity to a host plant and in many cases to a particular habitat. Even where there were highly indicative mollusc species present, they were frequently outnumbered by the catholic species. Consequently, there is a much greater likelihood of finding relatively uninformative catholic species in a fossil deposit than of finding true indicator species. This problem was exacerbated by the much higher concentration of molluscs from wetland sites than from dry woodlands. If the fossil deposit was lain down in an aquatic habitat the local aquatic molluscs will greatly outnumber those from the adjacent dry land. The best use of molluscs in such a circumstance would be to use them to estimate the aquatic conditions of the pool, e.g. the state of eutrophication, the weediness, the strength of flow, the oxygenation and the substrate material.

If there were any dry land taxa present these would probably be so scarce as to be statistically invalid. However, if present, they may give an important indication of the degree of shading in the local habitat.

The various palaeoecological techniques yield different but complementary results. The local accuracy of the propagule record adds detail to the broader regional representation of the pollen data. Molluscs can provide supplementary environmental information; particularly if there was a high proportion of dry land mollusca in the assemblage.

Alone, none of these techniques provided a perfect representation of the ecology of an area, but when combined the chances of misinterpreting the available data were much reduced, and a much richer image of the environment emerged.

CHAPTER 6: CHEMICAL, RADIOCARBON DATING AND SEDIMENT ACCUMULATION RATE RESULTS

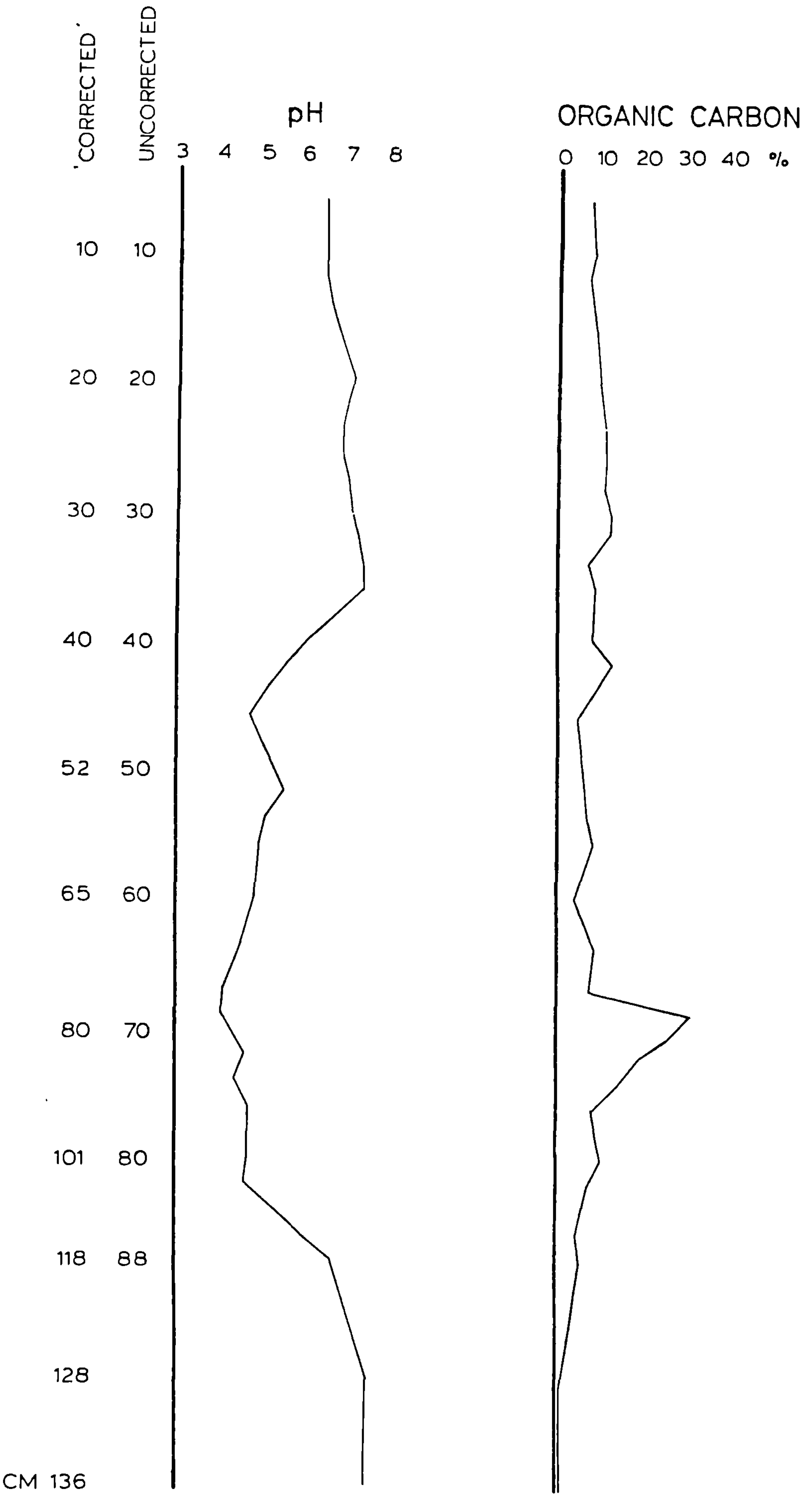
6.1 PH CONTENT OF SAMPLES

As can be seen from Fig. 6.1 the pH values in this deposit fall from 7.3 in the basal sample to 4.01 at 77 cm. The pH starts to fall immediately above the level at which peat formation began at 118 cm. The low pH might be a product of the decay of the mosses, and not an indication that the fen ever went acid. The waters feeding the fen from local springs and from the Gypsey Race would have been base-rich and it is likely that these waters would have maintained a relatively high pH at the surface of the fen. Above 46 cm there was a pronounced rise from 4.7 to pH 7.4 at 36 cm. Above this peak the deposit becomes slightly more acidic but is then relatively stable at c. pH 6.5, up to the present surface.

The acid reactions of some horizons probably accounts for the lack of mollusca at these levels. Mollusca were probably incorporated into the sediment but have since been dissolved.

The change in sediment stratigraphy at c. 48 cm is reflected in the pH. The silt component in sediments above this level was probably calcium-rich having been derived from an eroding topsoil in the catchment. The increasing pH provided a better environment for mollusc preservation accounting for the abundance of shells in these deposits.

FIG. 6.1 : pH AND ORGANIC CARBON (BY WEIGHT) IN THE POLLEN SAMPLES FROM WILLOW GARTH.



6.2 RESULTS OF ORGANIC CARBON ANALYSIS

It can be seen from Fig. 6.2 that the lowest samples in the profile, which were of the fluvially redeposited sandy clays, contained very little organic carbon (<1% by weight). With the onset of peat formation the carbon content rose to <u>c.</u> 6 - 10%. At 93 cm there starts a steady increase in the organic carbon content to a peak of 31%. Most of this increase is probably due to the presence of a timber-rich layer between 76 and 84 cm which is largely composed of <u>Salix</u> timber although some <u>Quercus</u> and <u>Alnus</u> wood is also present. After this peak the curve for organic carbon returns to a relatively consistent 8 - 12% of the total dry weight. At two points, at 67 cm and 46 cm, this value falls as low as 4%.

6.3 RESULTS OF THE RADIOCARBON ANALYSIS

The dates were as follows:

Code	Depth	Deposit	Date yrs B.P.
SRR-2665	8 - 10cm	Gyttja	110 ±0.6% Modern
			$d^{13}C$= -28.9^{o}/oo
		CO_3^{2-} present	($d^{13}C$= -7.1^{o}/oo
		but insufficient for age measurement.	
SRR-2666	16 - 18cm	Gyttja	700 ±50 (Organic)
			$d^{13}C$ = -29.2^{o}/oo
			3890 ±80 (Carbonate)
			$d^{13}C$ = - 5.3^{o}/oo

SRR-2667 26 - 28cm Gyttja 1170 $\pm$50 (Organic)
$d^{13}C = -28.6^{o}/oo$
5730 $\pm$80 (Carbonate)
$d^{13}C = - 3.1^{o}/oo$

SRR-2668 36 - 38cm Gyttja 1300 $\pm$50
$d^{13}C = -29.6^{o}/oo$
no measurable CO_3^{2-}.

SRR-2669 46 - 48cm Gyttja 2120 $\pm$50
$d^{13}C = -29.3^{o}/oo$
no measurable CO_3^{2-}.

SRR-2670 56 - 58cm Moss peat 3970 $\pm$50
$d^{13}C = -29.2^{o}/oo$
no measurable CO_3^{2-}.

SRR-2671 68 - 70cm Moss peat 8290 $\pm$80
$d^{13}C = -28.9^{o}/oo$
no measurable CO_3^{2-}.

SRR-2672 76 - 78cm Moss peat 8910 $\pm$80
$d^{13}C = -28.0^{o}/oo$
no measurable CO_3^{2-}.

SRR-2673 82 - 84cm Moss peat 9380 $\pm$80

$d^{13}C = -30.1^{o}/oo$

no measurable CO_3^{2-}.

SRR-2674 86 - 88cm Moss peat 9460 $\pm$80

$d^{13}C = -28.9^{o}/oo$

CO_3^{2-} present $d^{13}C = -2.9^{o}/oo$

but insufficient for measurement.

The organic fraction has consistently low values for the $d^{13}C$ analysis ranging from $-28.0^{o}/oo$ to $-30.1^{o}/oo$. Using these values, the ^{14}C dates can be corrected for isotopic fractionation and normalised relative to the value of $d^{13}C = -25^{o}/oo$. The dates obtained from the two 'carbonate' fractions from the gyttja samples produced much older dates than shown by the 'organic' carbon. This most likely results from the inclusion in these samples of chalk dust and old carbonate from mollusc shells. For this reason the more conservative 'organic ' carbon dates are used for the subsequent analyses.

The dates are plotted against depth in Fig. 6.3. As mentioned in the methods section the core obtained for palynological analysis and radiocarbon dating was, from 48 cm - 118 cm, subject to compaction. The monolith which was dug from the ground within 0.5 m of where the pollen core had been taken showed the same total depth of organic deposit as the known total depth of the pollen core and contained a similar stratigraphy. By correlating the boundaries of stratigraphic changes it is

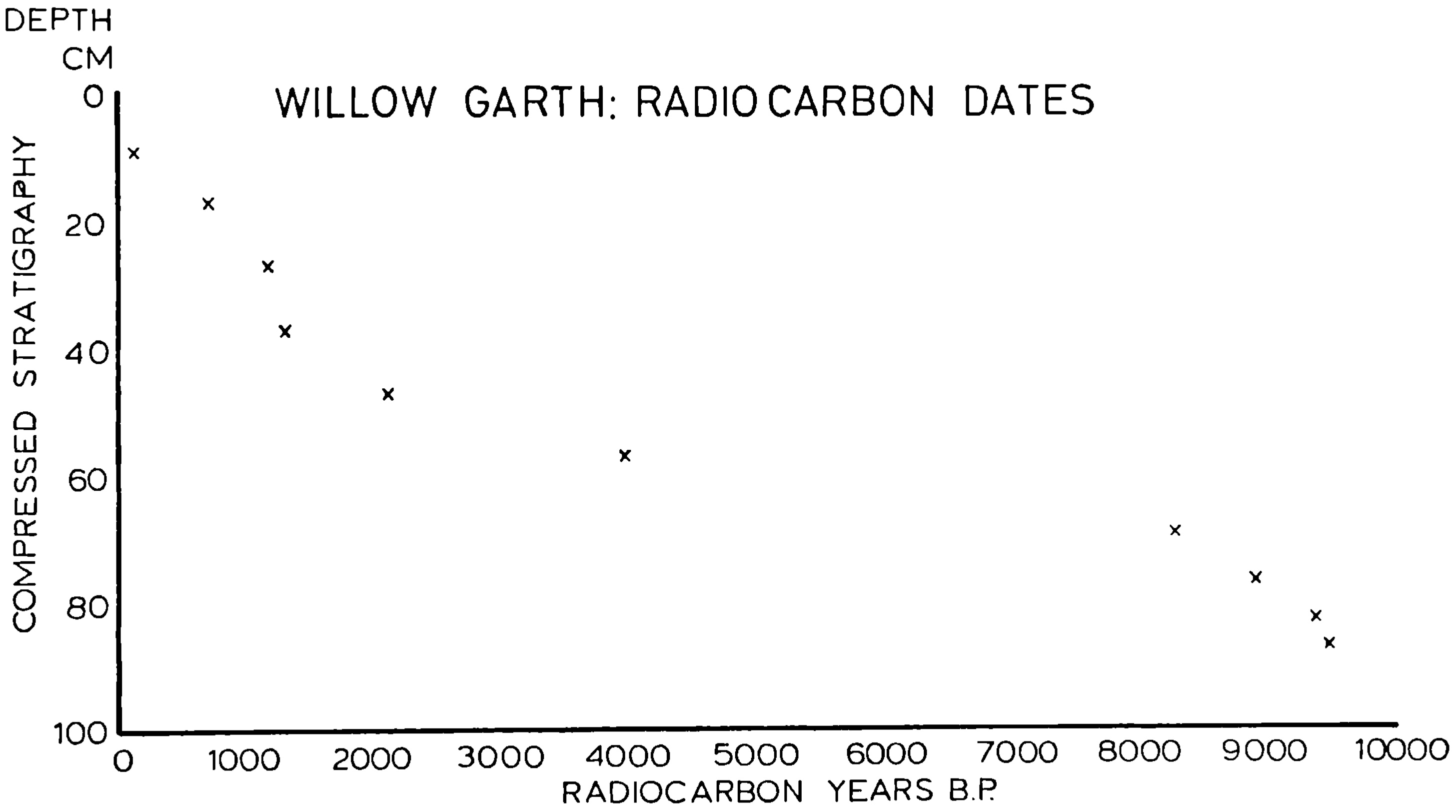


FIG. 6.2: RADIOCARBON DATES FROM WILLOW GARTH

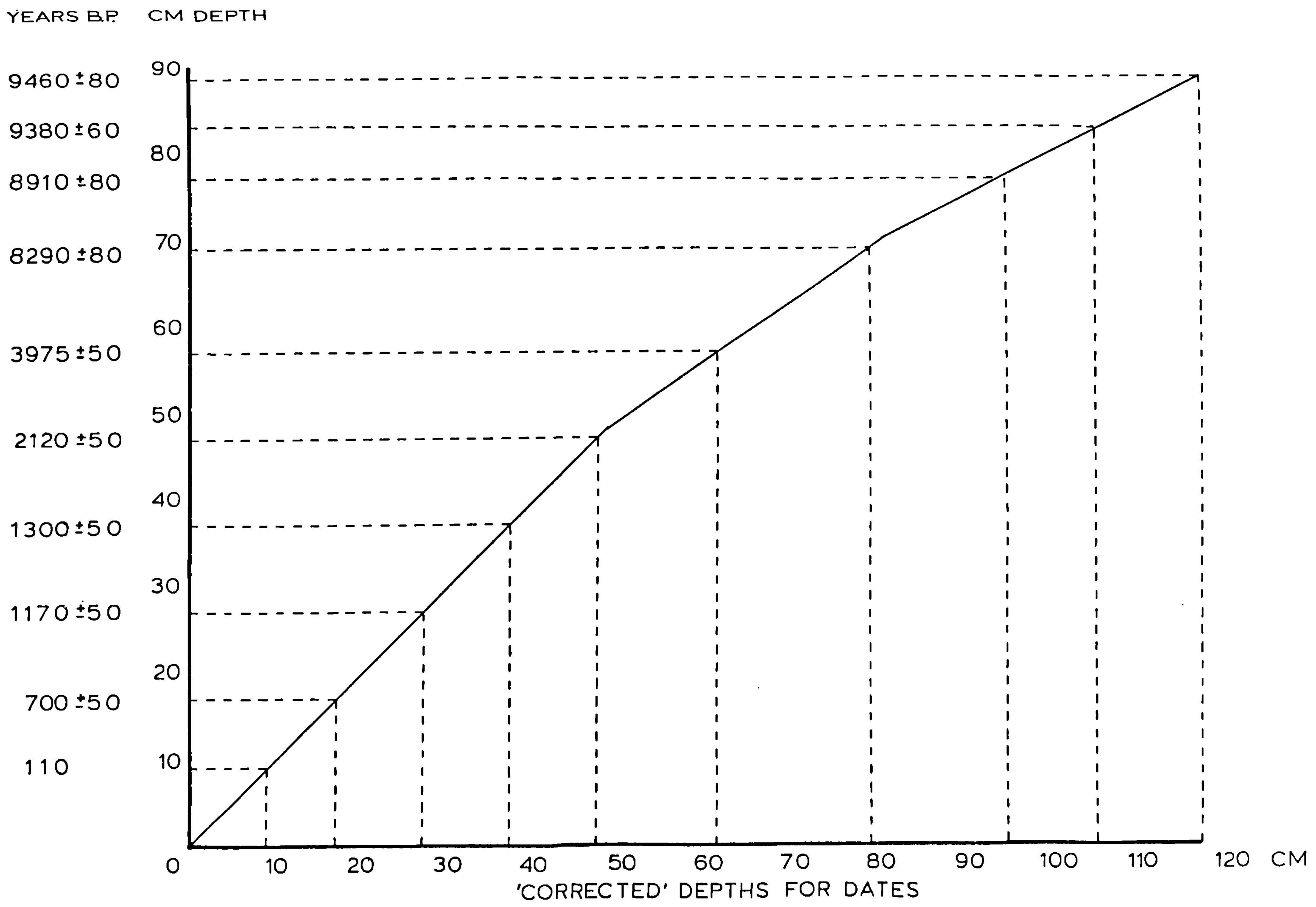


FIG. 6.3 : INFERRED RADIOCARBON DATES FOR THE SEDIMENTARY DEPOSITS AT WILLOW GARTH

possible to obtain a 'corrected' stratigraphy for the pollen core. This was done using the top of the moss peat at 47 cm, the layer of timber at 80 cm and the bottom of the peat at 118 cm. The resultant curve for the 'corrected' stratigraphy is shown in Fig. 6.4.

It must be recognised that this is an inferred stratigraphy and that the dates on the 'corrected' stratigraphy are also inferred. However, the 'corrected' stratigraphy will be used in all future discussion to render the macrofossil and palynological evidence comparable. To try to comment on two different stratigraphies would be unnecessarily confusing.

The dates when plotted using the 'corrected' stratigraphy, can be statistically proven to show a significant correlation with the regression line:

$X = -1424.35 + 100.35 \times Y$. Where X = Date and Y = Depth

The correlation coefficient (R) for this line is 0.97, giving an RSQ value of 0.94. The _t_ value is 11.27 with 8 degrees of freedom and so shows a probability of 0.001% that this is a chance distribution. If however the sediment stratigraphy is taken into account it becomes apparent that between 62 and 76 cm there is the passage of 4200 years implying a sediment accumulation rate of _c._ 0.0015 cm per year of a moss peat which appears identical to the moss peat below which had been accumulating at _c._ 0.027 cm per year. This seems unlikely particularly during the climatic optimum of the post-glacial. Although there is no visible change in the core in this zone it would appear that at some point between 62 and 76 cm there is a standstill level or hiatus in this core. The pollen stratigraphy

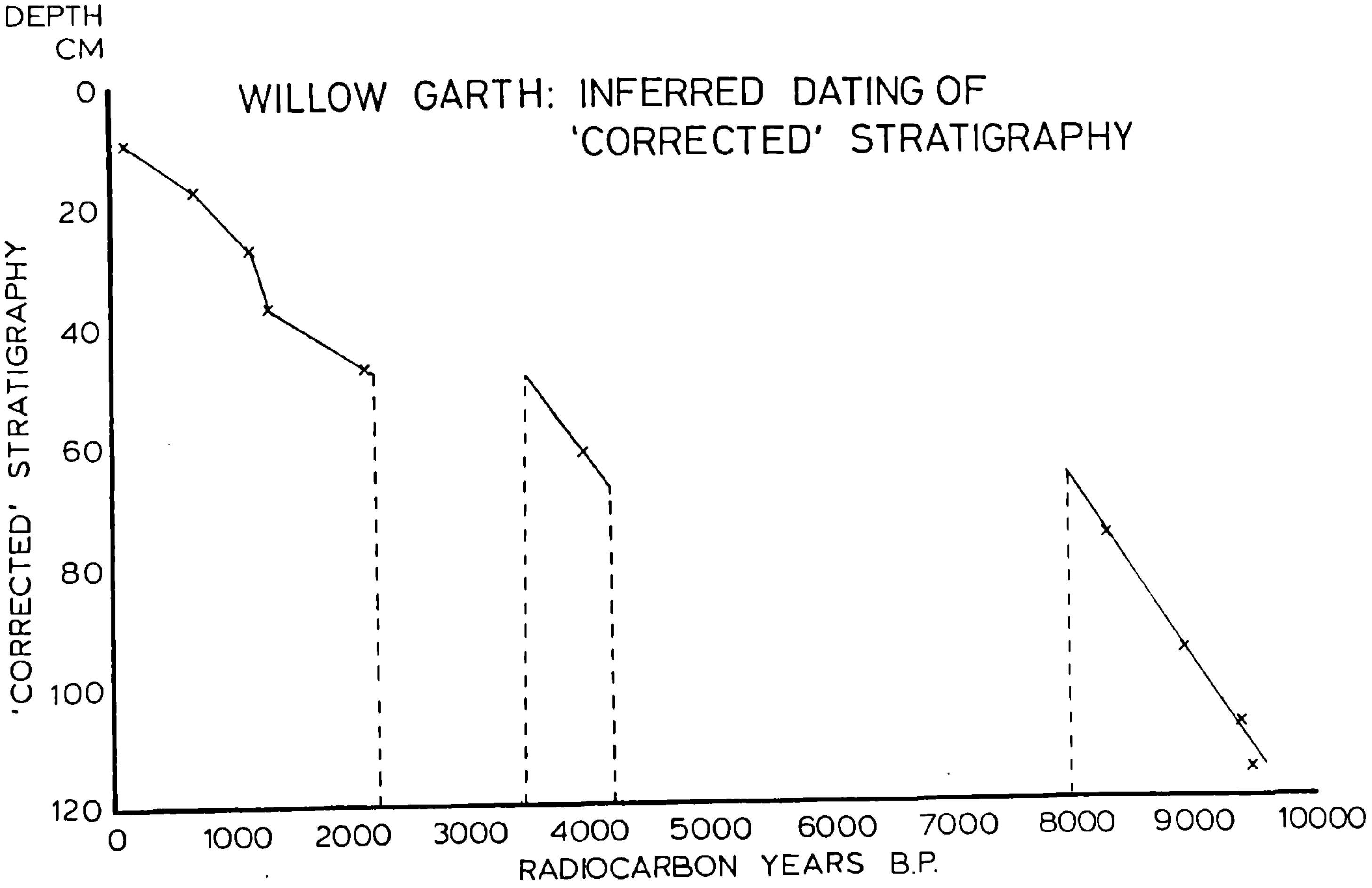


FIG. 6.4 : INFERRED RADIOCARBON DATING OF THE 'CORRECTED' STRATIGRAPHY SHOWING TWO INTERRUPTIONS IN THE SEQUENCE OF SEDIMENTATION.

shows a marked change of taxa at 67 cm and the hiatus is assumed to have taken place at this level.

If it is assumed that there is a break in the core at 67 cm a regression line can be placed through the four lowest points which are all taken from the same sediment type and may therefore represent a period of relatively constant deposition, as would be suggested by the radiocarbon dates. The best fit regression line through these points is:

$X = -178.51 + 0.03 \times Y.$ Where X = Date and Y = Depth

The R value for this regression was 0.98, RSQ was 0.97 and a t value of 7.79 with 2 degrees of freedom indicates a probability of 0.02% that this is a product of chance. Although the probability that this line is the result of a chance distribution of points is marginally higher than in the previous equation the uniformity of sediment in these four samples makes this a more reliable regression. Above these bottom four points the graph levels off very markedly, even if a hiatus at 67 cm is taken into account, and yet the sediment deposit from 67 - 48 cm is indistinguishable from that of the section below. This would suggest a similar environment of deposition and in all probability a similar rate of accretion between 67 and 48 cm. The local (macrofossil) vegetation zonation indicated a change in the local flora at 48 cm where there is a change in sediment from the moss peats to gyttjas. It seems likely that after deposition had restarted at 67 cm there was a period of peat growth, continuing as before, until there was another standstill level at 48 cm.

In order to establish the duration of the proposed discontinuities the regression line for the bottom four points is extrapolated up to 67 cm, giving a date of <u>c.</u> 7980 B.P. which is an estimate for the start of the hiatus. Only one ^{14}C date is available between 48 and 67 cm, that of 3970 ±50 B.P.(SRR-2670) at 60 cm which provides a point of reference. If it is assumed that there was a second hiatus, and that sediment accumulation had been consistent with the preceding period, a line may be extrapolated down from 60 cm to 67 cm giving a date of <u>c.</u> 4180 B.P. for the end of the hiatus. Similarly, to establish the bottom date of the upper hiatus the line may be extrapolated upwards to 48cm giving a date of <u>c.</u> 3400 B.P.. This may seem a rather crude way to estimate these dates but it seems better to assume that there are standstill levels in this core and try to allow for them, than to ignore them and interpret the core as a continuous record of sedimentation (Fig. 6.4).

6.4 HIATUSES A CAUSE FOR CONCERN?

In any deposit which may at some point have been subject to a period of drying out, and this includes almost all deposits other than deep lakes, there is a chance that deposition may have stopped altogether at that time. With the realisation that one radiocarbon date is not sufficient to date a core there an increasing number of studies which utilise as many as 30 radiocarbon dates on a single core.

Such dating greatly increases the accuracy with which the environmental record can be established, but it does not necessarily make the life of the palaeoecologist any easier! The more radiocarbon dates that are provided for a stratigraphic sequence the greater the possibility of uncovering weaknesses in the radiocarbon dating process itself, unexpected changes in depositional rates, or perhaps worst of all, sequences of inverted stratigraphy. In order to minimise errors from the radiocarbon assay most researchers will initially try to obtain all the dates from one laboratory. This should ensure that the laboratory techniques used are consistent.

Sometimes the results of the dating reveal so confusing a depositional record that the reliability of the deposit is called into question. Often it is only through the multiple dating of a core that such phenomena become apparent. Liu et al., (in press) obtained 19 dates from a 7 m core from Yunnan, S.W. China. Each date added to the complexity and contortion of the sedimentary history and yet had the first date been accepted then a perfectly 'normal' palaeoecological record could have been induced (Walker pers. comm.).

When multiple dates are obtained on a stratigraphic sequence they seldom fall on a straight line or even on a regular curve. The danger of fitting a best fit regression line, heedless of the stratigraphy, can be illustrated by the dates obtained in this study. The ten dates obtained (and even an eleventh from the preliminary study) will fit closely to a regression line. The value of t and of the correlation coefficient give no indication that such a practice would be grossly misleading. It is only when the litho- and bio-stratigraphies are taken into account that it becomes apparent that an hiatus exists.

Before the use of multiple dating, when the only indication of an hiatus was a band of mineral matter in the core, or abrupt changes in pollen values, it is likely that many standstill levels were overlooked.

With the increased use of radiocarbon dating more stratigraphic sequences are showing apparent pauses in deposition which do not correlate directly with periods of mineral inwash. In the study of Cranberry Bog, Co. Durham, Turner and Kershaw (1973) noted that the whole of pollen zone VII was missing and yet there was little stratigraphic evidence to indicate this. In another case, which has some close parallels with the present study, Janssen (1967) analysed deposits from Stephen's Lake, a small _Typha_ swamp in Minnesota. The lake, which formed in a small basin lined with calcareous till, presented an apparently entire post-glacial history of the local vegetation although the deposit was only 114 cm deep. The deposit was composed of a mixture of woody peat and _Drepanocladus_ peat. Janssen suggested that the depositional process at this site may have been interrupted by a mass of small hiatuses, due to the oxidation of the surface samples, which left no stratigraphic trace in the core. Clearly, such a process could lead to the selective preservation of pollen which would distort pollen influx data. Janssen recognised that an hiatus in itself was not a serious problem in the interpretation of a pollen sequence, so long as there had not been reworking of sediments.

At Willow Garth the post-glacial warming resulted in the formation of a fen in which accumulated a moss peat but between _c._ 7900 B.P. and 4200 B.P. an event occurred which either prevented any further depositional development, or mechanically eroded the uppermost portion of the peat deposit, or chemically oxidised the upper layers of the peat. Alternatively accumulation and oxidation might have proceeded continuously but at equal rates.

Mechanical erosion, e.g. by a stream, would almost certainly have cut right through the peat deposit or have left some trace of the former channel, e.g. a strongly mineral layer. Despite a slight reduction in the organic carbon content of the core at the time of the hiatus there is no layer of sands and gravels as one would expect from an erosive stream. Peat cutting by man has not been recorded as early as this elsewhere in Britain.

If the water-table were to fall then oxidation of the surface samples would follow. The exposed layers of the peat would break down and be lost from the record. That this hiatus came as the result of a single event at 4200 B.P. might be considered as unlikely. Assuming a constant rate of peat accumulation 89 cm of peat would have formed in the period from 7900 - 4200 B.P.. The water table would have had to drop by this much for the peat to have been oxidised. It is more reasonable to suppose that the period represented by the standstill was one of a locally stable water table in which a few years peat growth would be oxidised by a succession of dry summers. In this way there was no net peat growth but the fen never dried sufficiently for the sub-surface samples to become oxidised.

At c. 4200 B.P. the peat growth recommenced due to the resumption of a wetter regime until c. 3400 B.P.. The similarity of this deposit to the peat below thehiatus suggests that the source of water was the same as before.

A second hiatus which, unlike the first, is marked by a change in the stratigraphy could represent another cessation of peat growth in the same manner. Although the moss peat gives way to an organic rich mud there is no evidence of scouring or fluvial erosion. It is suggested that once again a balance between peat growth and oxidation had been reached. In this instance, however, whatever brought about the change in the local stratigraphy was also responsible for altering the local hydrology as indicated by the change in sediment type. This may possibly have been caused by drainage being impeded by the erosion of topsoil within the watershed.

The hiatus which lasted from 3400 B.P. to 2200 B.P. would correlate well with the prominent <u>grenzhorizont</u> surface reported by Godwin (1975). Godwin listed 12 sites with a recurrence surface at <u>c.</u> 3300 to 2200 B.P.. Thus, this may represent a period of reduced rainfall during the Flandrian, as it would still be early for loss of peat due to peat cutting.

Whilst the presence of an hiatus in a sedimentary sequence may be frustrating, covering important periods of ecological change, it does not necessarily indicate disturbance or reworking in the profile and may not therefore invalidate the results from the site.

6.5 SEDIMENTATION ACCUMULATION RATES

The hypothesis that two hiatuses are present in the core is utilised for the calculation of sedimentation rates. Two values are presented, calculated using the equations in section 3.6.1

The following values were obtained:

cm depth	yr per cm	cm per yr
0 - 9	12.2	0.0818
10 - 17	84.3	0.0119
18 - 27	47.0	0.0213
28 - 37	13.0	0.0769
37 - 47	82.0	0.0122
48 - 67	37.0	0.0270
68 - 118	37.0	0.0270

These data could then be used to obtain the pollen influx, the formula for which was given in section 3.6.2

CHAPTER 7: THE ANALYSIS OF FOSSIL ECOLOGICAL DATA

In this chapter the zonations of pollen, plant propagule and molluse diagrams are described. The ordination of these samples by DECORANA is also considered and a comparison between ordination diagrams for the various data sets is made. The modern analogue and fossil data are displayed in the ordinations in order to facilitate the interpretation of these data in the following chapter.

7.1 ZONATION OF POLLEN DATA

POLZON (Gordon and Birks, 1972) and TWINSPAN (Hill, 1979a) are both classificatory techniques, but whereas POLZON is constrained to compare neighbouring levels, TWINSPAN will provide an unconstrained classification. The results of the TWINSPAN classification show that even though unconstrained this program produced blocks of sequential levels as the product of its analysis.

The divisions arrived at from POLZON varied according to the method which had been used (see chapter 4). Shown below are the results of the zonation of the fossil pollen data from Willow Garth (Table 7.1).

TWINSPAN	CONSLINK	SPLIT INF	SUM SQ	BOUNDARY
			20	
32				
	34	34	34	*
51	51	51		*
		54	54	
67	67	67	67	*
	69			
76				
95	95	95	95	*
		98		
			99	
	102			
104				
	106	106	106	*
114				
128	128	128	128	*
132	132	132	132	*

Table 7.1 Results of the zonation of fossil pollen data
Figures are sediment depths in cm and 'BOUNDARY' indicates adopted zone boundaries

Where all three methods of the POLZON analysis agreed on the definition of a zone boundary then the boundary was accepted. Where two out of the three agreed, as in the case of the proposed zone boundary at 51 cm or 54 cm then whichever appeared to be of the most ecological value, as both were of equal statistical value, was adopted. For this reason 51 was adopted in preference to 54. The Twinspan classification although not utilised for the purposes of zonation produced a very similar scheme of boundaries with the five major boundaries at 67 cm, 95 cm, 106 cm, 128 cm, and 132 cm all identified.

7.2 PLANT PROPAGULE ZONATIONS

The zonations obtained for the plant propagules data were as shown in Table 7.2.

TWINSPAN	CONSLINK	SPLIT INF	SUM SQ	BOUNDARIES
	4			
	8	8	8	*
16	16	16	16	*
	20	20	20	*
	28	28	28	*
44		44	44	*
		52		
	68		68	*
	72			
	76	76	76	*
84		84	84	*
108				
		112	112	*
		124	124	*
128	128			
	132			

Table 7.2 Results of zonation of fossil propagule data
Figures are sediment depths in cm and 'BOUNDARY' indicates adopted zone boundaries

It can be seen from the above data that of the five zones selected by all three statistical techniques within POLZON, four are in the top section of the core and only one, at 76 cm, in the lower section. This suggests that the most significant local vegetational changes have been taking place within the time represented by the top 30 cm of the core. Prior to that period the only major change in the local vegetation indicated by this analysis took place at 76 cm. The other divisions have been adopted on the basis of two out of three tests indicating a zone boundary at that position.

7.3 GRAMINEAE SIZE DATA

Results of this zonation analysis are given in Table 7.3.

CONSLINK	SPLIT INF	SPLIT SQ	BOUNDARY
8		8	*
26		26	*
	28		
34		34	*
		46	
48			
51	51		*
	68		*
		70	
	106	106	*
	132	132	*

Table 7.3 Results of the zonation of Gramineae pollen size data. Figures are sediment depths in cm

The three methods produced zonations which have little in common, although there seem to be boundaries at the points shown above on the basis of two out of three zonations agreeing, or the boundary being placed in neighbouring levels.

7.4 MOLLUSC DATA

Results of the zonation of the mollusc data are given in Table 7.4.

CONSLINK	SPLIT INF	SPLIT SQ	BOUNDARY
16	16	16	*
24	24	24	*
44	44	44	*
124	124	124	*

Table 7.4 Results of the zonation of fossil mollusc data
Figures represent sediment depth in cm and
'BOUNDARY' indicates adopted zone boundaries.

These results present no problem as there is total agreement as to the adoption of the four zone boundaries. The four stratigraphic zones were sufficient as there was no mollusc record of statistical value between 44 cm and 120 cm.

7.5 COMPARISON OF ZONATIONS

The comparison of the pollen zonation, which probably represents an extra-local and regional vegetation assemblage, and the macrofossil data, which will have been primarily derived from within a few metres of the site, will yield information on whether vegetation changes recorded in the fossil sequences were local or regional events. That the macrofossil record may have been supplemented by some species being washed into the deposit is a possibility which should not be overlooked. The good state of macrofossil preservation, and the close environmental correlations obtained from the various strands of macrofossil evidence would argue against a high proportion of this material having been transported from a different environment. If the zonation of the plant propagule record indicates a boundary where none occurs in the pollen record this might be interpreted as a purely local change in the vegetation. If, on the other hand, there is a change in the pollen stratigraphy which is not matched in the macrofossil assemblage then this would indicate a change in the regional flora which did not affect the fen vegetation. If a zone boundary changes in both at the same time this could indicate one of two things. Either that there is a major widespread event of sufficient magnitude to affect both the reginal and the local vegetation, or that it is a very marked local change, strong enough to influence the pollen deposition as well as the macrofossils.

7.5.1 Comparison of the Zonation of Fossil Gramineae Pollen, Fossil Pollen and Fossil Propagule data

Due to the pollen and propagule samples being taken at different spatial intervals, pollen at 2 cm or 1 cm intervals and macrofossils at 4 cm intervals, the pollen zone boundaries may fall within a macrofossil layer and so the zonation may be the same even if the levels do not coincide precisely. For this reason a statistical test to ascertain which pair of zonations is the most similar would not be valid. Any such similarity must be sought subjectively.

GRAMINEAE POLLEN	POLLEN	PROPAGULES
8		8
		16
		20
26		
		28
34	34	
		44
51	51	
68	67	68
		76
		84
	96	
106	106	
		112
		124
	128	
132	132	

Table 7.5 A comparison of zonations for fossil samples.
Numbers indicate sediment depth in cm.

From Table 7.5 it may be seen that only one level, that of 67 - 68 cm shows a change which affected all the stratigraphies. This level is at the point of the major discontinuity in the sedimentary history of the site. It is not surprising to find that such a boundary would be evident in both the pollen and macrofossil records.

The biozones used in the discussion section are based on the pollen stratigraphy, although sub-zones are utilised where there appears to be an event of ecological importance indicated by the macrofossil zonation.

The zonation of the Gramineae size data offers a further independent zonation. Only three levels are in common with the macrofossil data, one of which is the level of the hiatus and is also common to the pollen zonation. The other two both occur in the top part of the core which represents a time when, it will be shown, there was a drier environment and grasses may have encroached further onto the fen. In the levels below 30 cm the zonation of the grasses is far more similar to the pollen zonation than that of the macrofossils. This suggests that a significant proportion of the Gramineae pollen was derived from the extra-local and regional vegetation. Therefore changes in the Gramineae levels within this core are important, particularly during the early stages, as they probably reflect changes in the extra-local grasslands rather than the fen.

7.6 BIOSTRATIGRAPHY

7.6.1 Pollen Stratigraphy

Unless specifically stated all percentages are expressed as the percentage of dry land pollen.

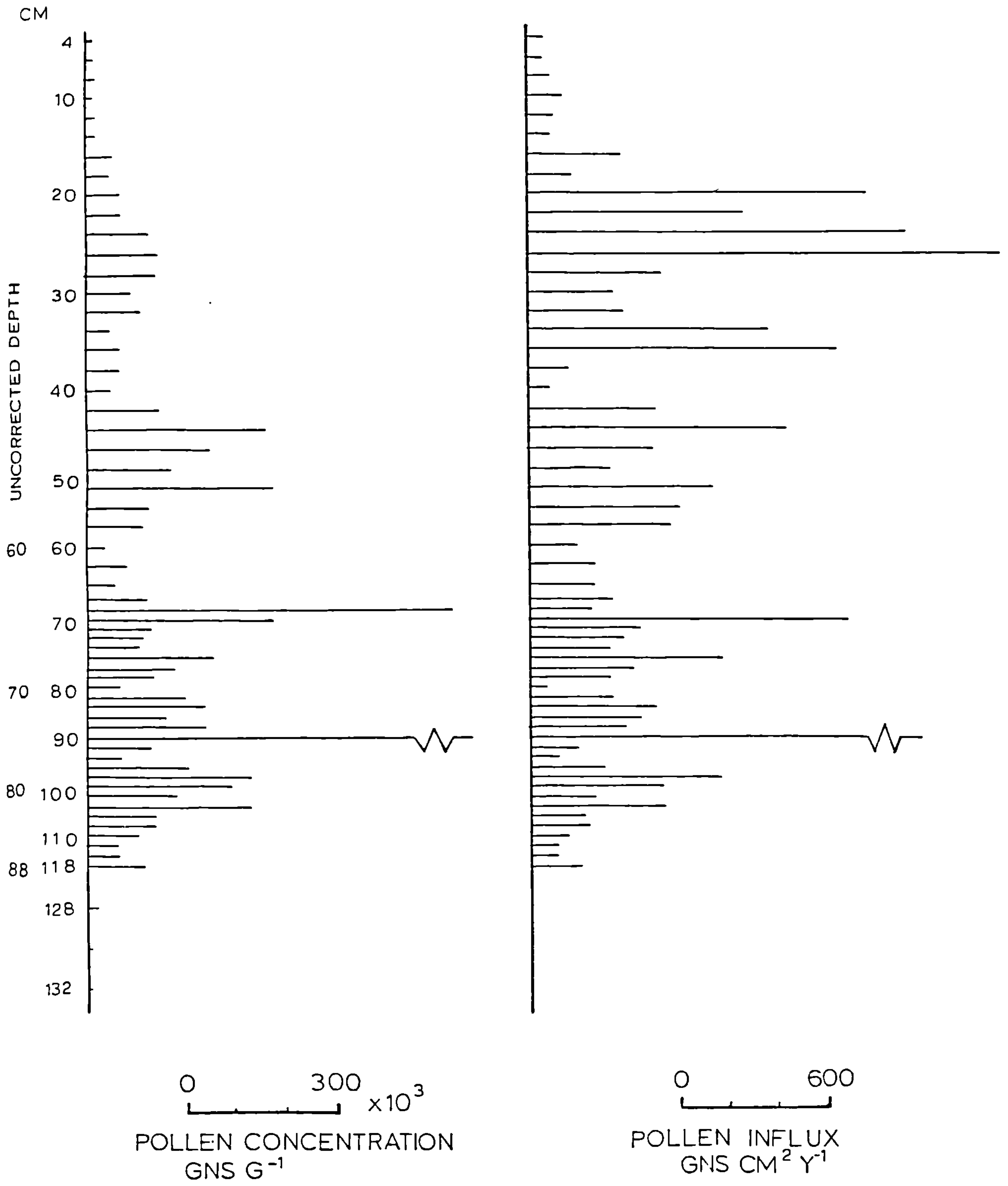
WGP-1 (136 - 133 cm)

Pollen concentration in this zone is low with 27790 grains g^{-1} (Fig. 7.1), but there is a high species diversity with 45 pollen and spore taxa identified. *Betula* (19.5%), *Salix* (16.1%) and *Pinus* (8.6%) are the dominant arboreal taxa (Figs. 7.2 and 7.3). A single grain of *Alnus* and 7 of *Corylus* were also recorded. The pollen of the shrubs *Juniperus*, *Betula nana* and *Empetrum* was present, totalling 7% of the dry land pollen sum. Open ground species were abundant including: *Geranium*, *Thalictrum*, *Lychnis*, Liguliflorae, *Filipendula*, *Potentilla* and *Achillea* type. Gramineae (24%) dominated the non-arboreal component and values for Cyperaceae pollen are low (10%). Obligate aquatics included *Myriophyllum* spp., *Callitriche* and *Typha latifolia*; these combine to total 2%. Also present were *Saxifraga oppositifolia*, *Saxifraga aizoides*, *Dryas*, *Armeria* and *Plantago maritima*, a cold, dry or montane group which total 4%. *Equisetum* spores were scarce (2.9%) and *Athyrium* was present at less than 1%, as were *Selaginella selaginoides* and *Botrychium lunaria*.

WGP-2 (132 - 129 cm)

The pollen concentration in this level was very low, 5485 grains g^{-1}. The only abundant arboreal taxon was *Pinus* (28.5%); tree Birch was scarce (<1%). The only 2 shrub taxa represented were *Empetrum* and *Juniperus* which together only reached 1.6%. The pollen sum was dominated by herbaceous taxa with Gramineae (48.2%) as the commonest of all. *Armeria*, *Campanula*, *Gentiana verna*, *Gentiana pneumonanthe* and *Lychnis* were all present at less

FIG. 7.1: SUMMARY DIAGRAM OF POLLEN INFLUX AND CONCENTRATION FROM WILLOW GARTH



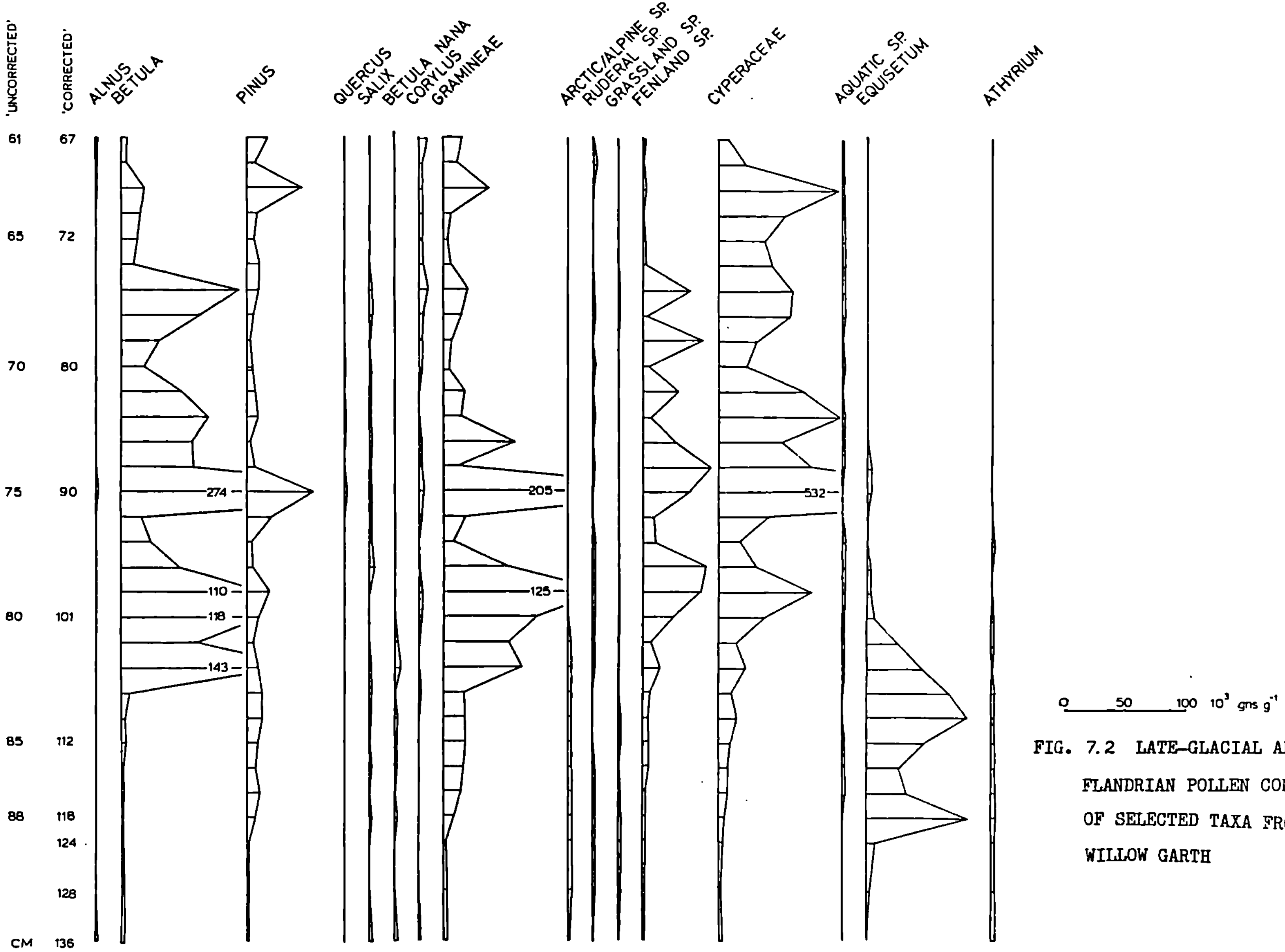


FIG. 7.2 LATE-GLACIAL AND EARLY-FLANDRIAN POLLEN CONCENTRATION OF SELECTED TAXA FROM WILLOW GARTH

than 2%, whilst Liguliflorae attained a high value of 11.9%. Cyperaceae pollen was increased in abundance at 25% and the spores of Botrychium lunaria, Athyrium and Lycopodium alpinum were also recorded.

WGP-3 (128 - 107 cm)

Pollen concentration increased progressively throughout this zone from 10000 to 187000 grains g^{-1}, whilst pollen influx ranged from 103 to 203 grains cm^2 y^{-1} (Figs. 7.1 and 7.4).

Pinus again dominated the arboreal pollen component with values from 24% to 36% whereas Betula did not exceed 13%. The shrubs present included Empetrum, Juniperus, Arctostaphylos and Betula nana, of which Empetrum was the most consistently occurring taxon. Salix pollen was also present in 5 out of 6 levels and one grain of Quercus was also recorded from this zone. The non-arboreal taxa formed 70% of the total dry land pollen and as in previous samples Gramineae was the best represented with 37 to 53%. Liguliflorae diminished steadily from 10% to 2%. Menyanthes was present in all the samples, as was Helianthemum. Saxifraga aizoides was present in 4 out of 6 samples. The flora was diverse but that diversity was decreasing throughout this zone. Polygonum viviparum and Polemonium caeruleum occurred for the first time in this zone. The pollen of obligate aquatics had a slight peak in this spectrum, but the Cyperaceae were constant at c. 20% to 23%. Athyrium increased to a maximum of 18% and Botrychium was present at 1% in all the samples in this group. Equisetum rose from 6% in WGP-2 to a maximum of 392% in this

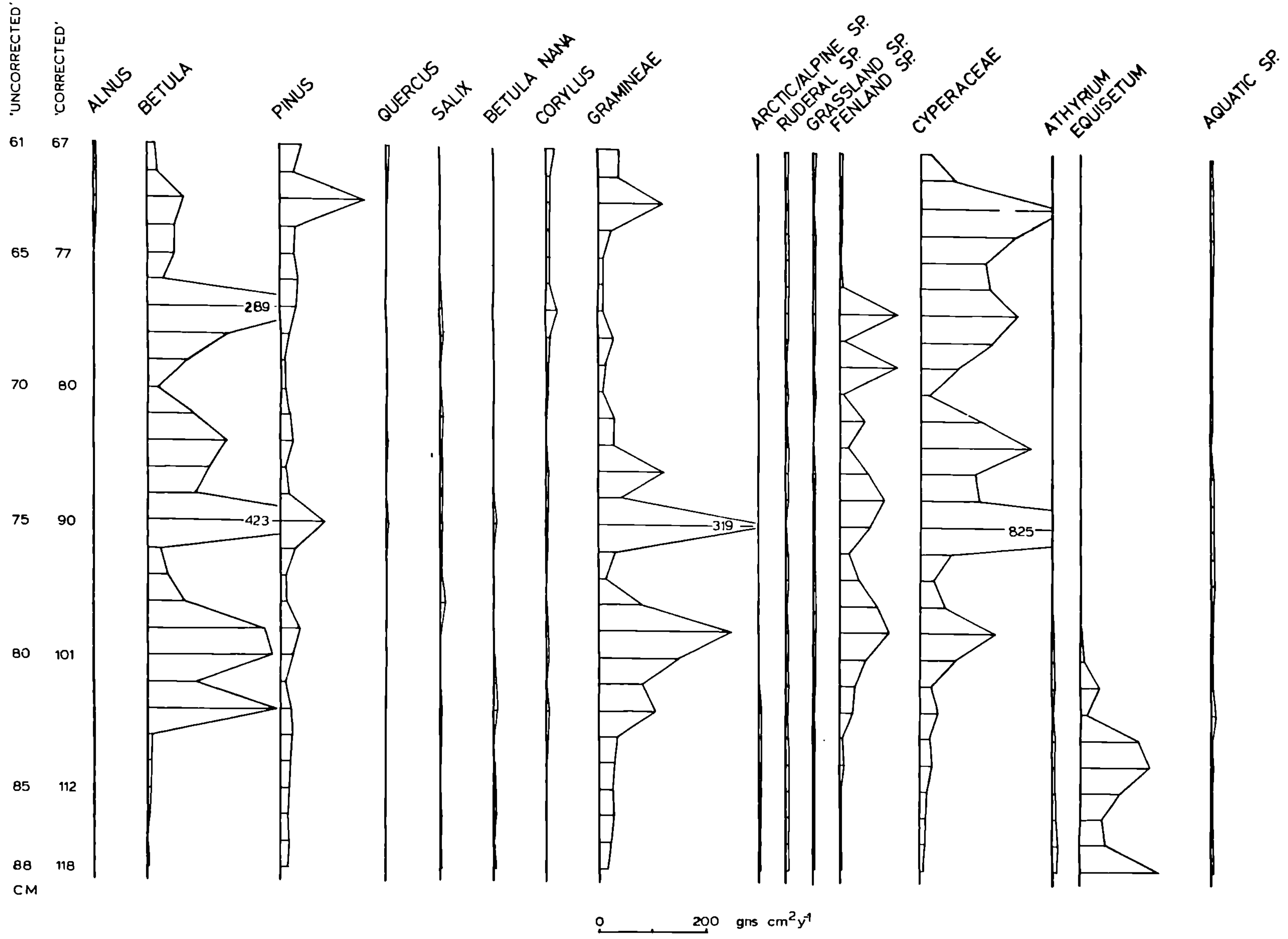


FIG. 7.4 LATE-GLACIAL AND EARLY-FLANDRIAN POLLEN INFLUX OF SELECTED TAXA TO WILLOW GARTH

zone.

WGP-4 (106 - 97 cm)

The pollen influx to this zone was higher than in the previous levels. A range of influx values from c. 270 to 770 grains cm^2 y^{-1} was recorded corresponding to pollen concentration values of 150000 to 400000 grains g^{-1}.

A rapid increase in Betula pollen to 58% is followed by a slight decline to c. 30%. Pinus pollen was present but much reduced at c. 3 to 5%. Gramineae pollen after falling to a minimum of 155 recovered to account for 30% at the end of this zone. This increase was matched by Menyanthes, increasing from 5% to 28% of the total dry land pollen. Liguliflorae was lost from the herb flora as were the indicators of cold dry conditions. Equisetum was much reduced with values falling to 1.2% There was a continued decrease in species diversity from 35 pollen and spore taxa in the basal sample to 17 taxa in the uppermost samples of the zone.

WGP-5 (96 - 68 cm)

The pollen and spore influx to this zone varied widely with values from 120 to 1,970 grains cm^2 y^{-1} and the concentration lay between 70,000 and 1,270,300 grains g^{-1}. These pollen concentration values seem very high but this fits with the slow sediment accumulation rate. Species diversity was relatively constant during this zone at c. 26 taxa in most levels.

After decreasing to a low of 24% at 93 cm Betula gradually recovered to 68%, then declined to c. 30%, recovered to 55%

and then declined once again to 18%. Salix occurred in 10 of the first 11 levels in this zone, though never accounting for more than 2% of the total. Alnus and Quercus were recorded with increasing regularity as the zone progressed. Pinus pollen showed two peaks during this zone. The first represented an increase from 2 to 28% and reached its peak at 89 cm. This peak ended abruptly and Pinus was present at less than 8% throughout the middle of this zone. Between 73 cm and 68 cm Pinus rose to a peak of 44% in samples which are pollen-rich. Gramineae fluctuated between 4 and 38%. Filipendula was also highly variable with values between <1% and 48%. Four consecutive levels (93 - 87 cm) contained Gramineae pollen grains larger than 46 µm diameter. Two of these were provisionally identified as Hordeum or Avena. Plantago lanceolata, Urtica dioica and Rumex all occurred in the same levels. Two grains of Teucrium botrys pollen were recorded from 75.5 cm. It was during the second Pinus peak that the arboreal pollen reached its peak in the entire diagram with 82% of the dry land pollen sum. This dominance was brief as Gramineae pollen increased during the last three samples of this zone from 11% to 36% and Liguliflorae returned as a consistent member of the assemblage.

Botrychium lunaria was present in the two lowest levels of this assemblage but was absent thereafter. At the top of the zone Cyperaceae were increasingly abundant with a peak of 140%. In the same samples Filicales attained values of 88%

WGP-6 (67 - 54 cm)

The boundary between WGP-5 and WGP-6 was the first division selected by the three POLZON programs and the TWINSPAN analysis.

Pollen influx rates to this zone were between 190 and 600 grains cm^2 $y^{-1}$and the concentrations were between 80,000 and 150,000 grains g^{-1} (Figs. 7.5 and 7.6). An increase in species diversity led to a peak of 54 pollen and spore taxa at 56 cm.

The zone is characterised by a marked decrease in *Betula* to values of *c.* 3% to 5%. *Alnus* reached a peak of 28% at 62 cm and *Corylus* reached a maximum of 27% at 58 cm. *Tilia* pollen was consistently present at 1% to 2.5%. Arboreal pollen accounted for *c.* 30% of the dry land pollen sum. Gramineae (25% to 30%) are abundant and undoubted *Cerealia* pollen (*c.* 1% to 3%) occurred for the first time. *Aphanes*, *Polygonum aviculare* and Chenopodiaceae are present. *Pinus*, Cyperaceae and *Filicales*, the commonest taxa at the end of the previous zone, are all low.

WGP-7 (52 - 36 cm)

Pollen influx ranged from 90 to 1,050 grains cm^2 y^{-1} and concentration from 44,000 to 360,000 grains g^{-1}. High species diversity was maintained throughout this zone.

Quercus, *Alnus*, *Salix* and *Corylus* were the predominant arboreal taxa but only total 11% to 17% of the pollen sum. Gramineae (25% to 40%) and Cruciferae (up to 19%) were the commonest herb taxa. *Cerealia* (1% to 4%) and associated weeds including *Centaurea cyanus* were also present. *Sanguisorba minor*, *Linum catharticum*, *Hypericum* and *Plantago media/major* occurred in low numbers throughout this zone. *Plantago lanceolata* had a brief

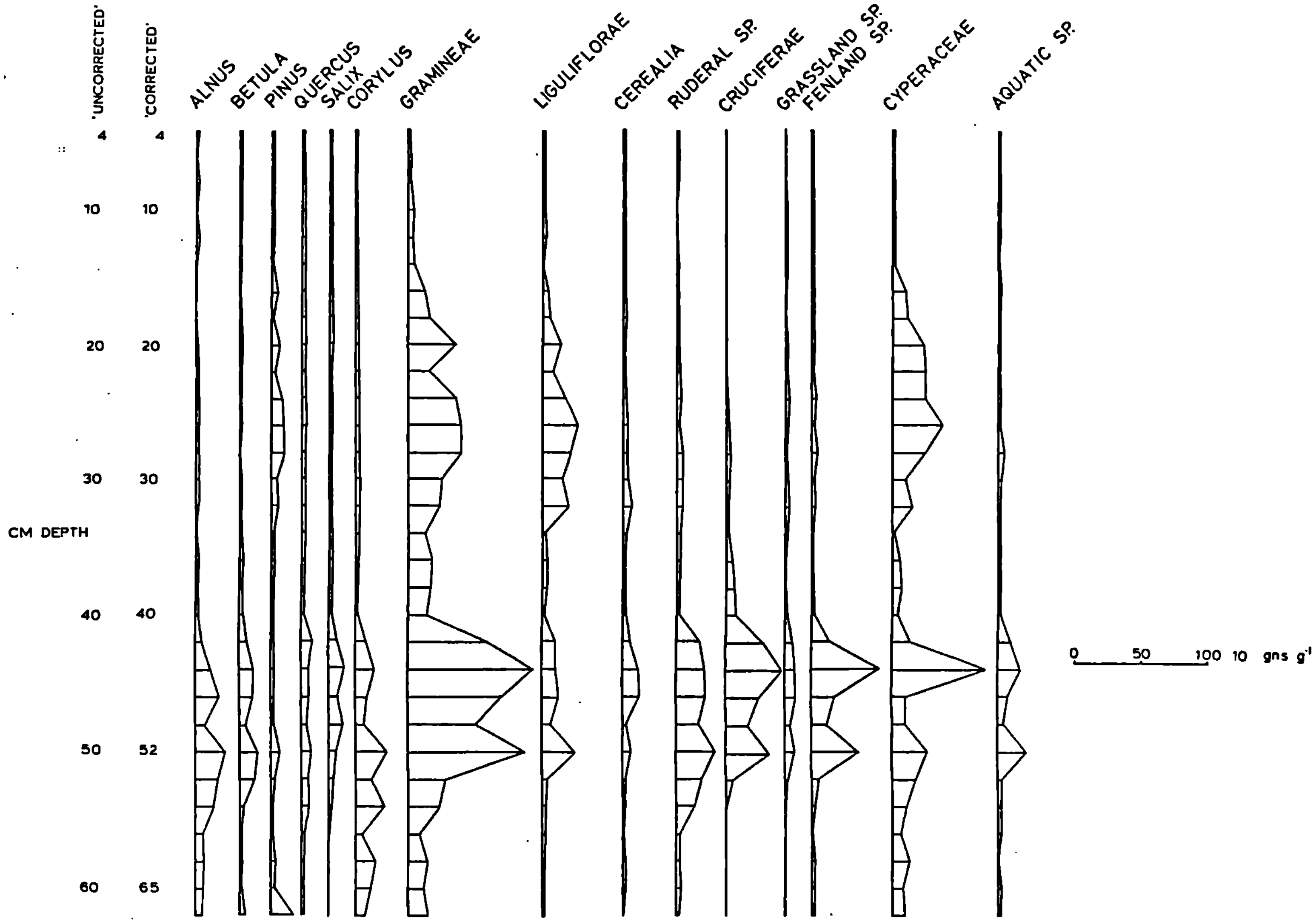


FIG. 7.5 MID- TO LATE-FLANDRIAN POLLEN CONCENTRATIONS OF SELECTED TAXA AT WILLOW GARTH

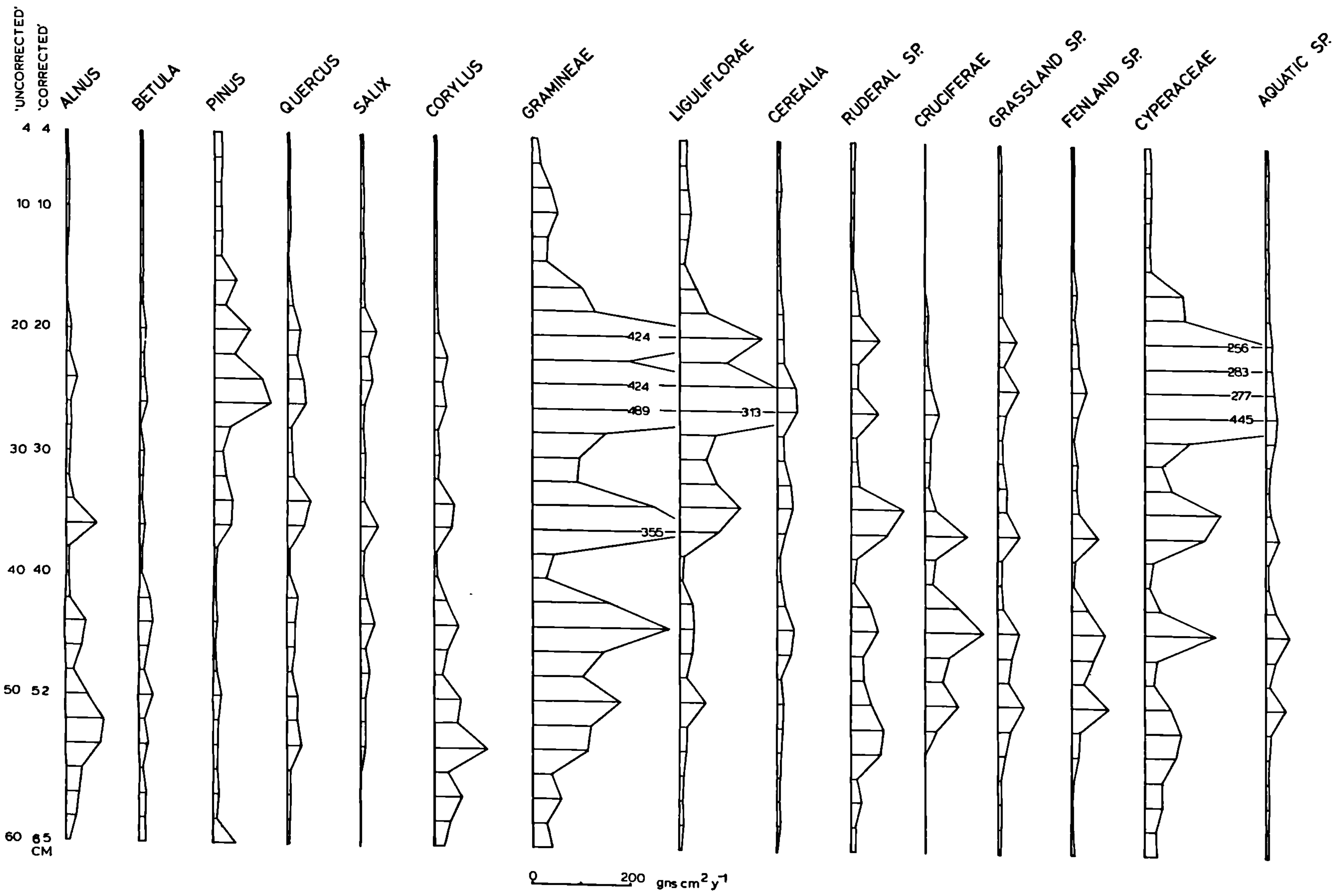


FIG. 7.6 MID- TO LATE-FLANDRIAN POLLEN INFLUX OF SELECTED TAXA TO WILLOW GARTH

rise to 11% at 52 cm and thereafter declined to *c.* 1% to 2%. The pollen of both the fen and the obligate aquatic flora was lower than in the previous zone.

WGP-8 (34 - 0 cm)

The five uppermost samples were poorly preserved with concentration values of less than 10000 grains g^{-1}. At a greater depth the influx was *c.* 350 to 1900 grains cm^2 y^{-1}. Concentration was *c.* 150,000 grains g^{-1}.

This zone had similar pollen spectra to the previous one; Gramineae (45%), Cyperaceae (15% to 40%), *Cerealia* and an abundance of disturbed ground indicator species were present. Liguliflorae pollen was abundant (10% to 20%). *Tilia*, virtually absent fom the last zone, was present in all samples, but often as a single grain in each count. *Pinus* pollen was abundant in the samples where there were low pollen concentrations. *Gentianella* pollen occurred for the first time, as did spores of *Osmunda* and *Thelypteris*.

7.6.2 Plant Macrofossil Stratigraphy

WGS-1 (136 - 125 cm)

The concentration of the fruits and seeds in this zone increased from 35 to 106 fruits per litre of sediment (Fig. 7.7 and 7.8). Obligate aquatics (12% to 38%) were abundant including: *Potamogeton* spp., *Ranunculus* sec *Batrachium* and *Callitriche*. *Menyanthes trifoliata* (4% to 16%) and other fenland taxa e.g. Cyperaceae undiff (4% to 30%) and *Carex* cf. *riparia* (4%) were

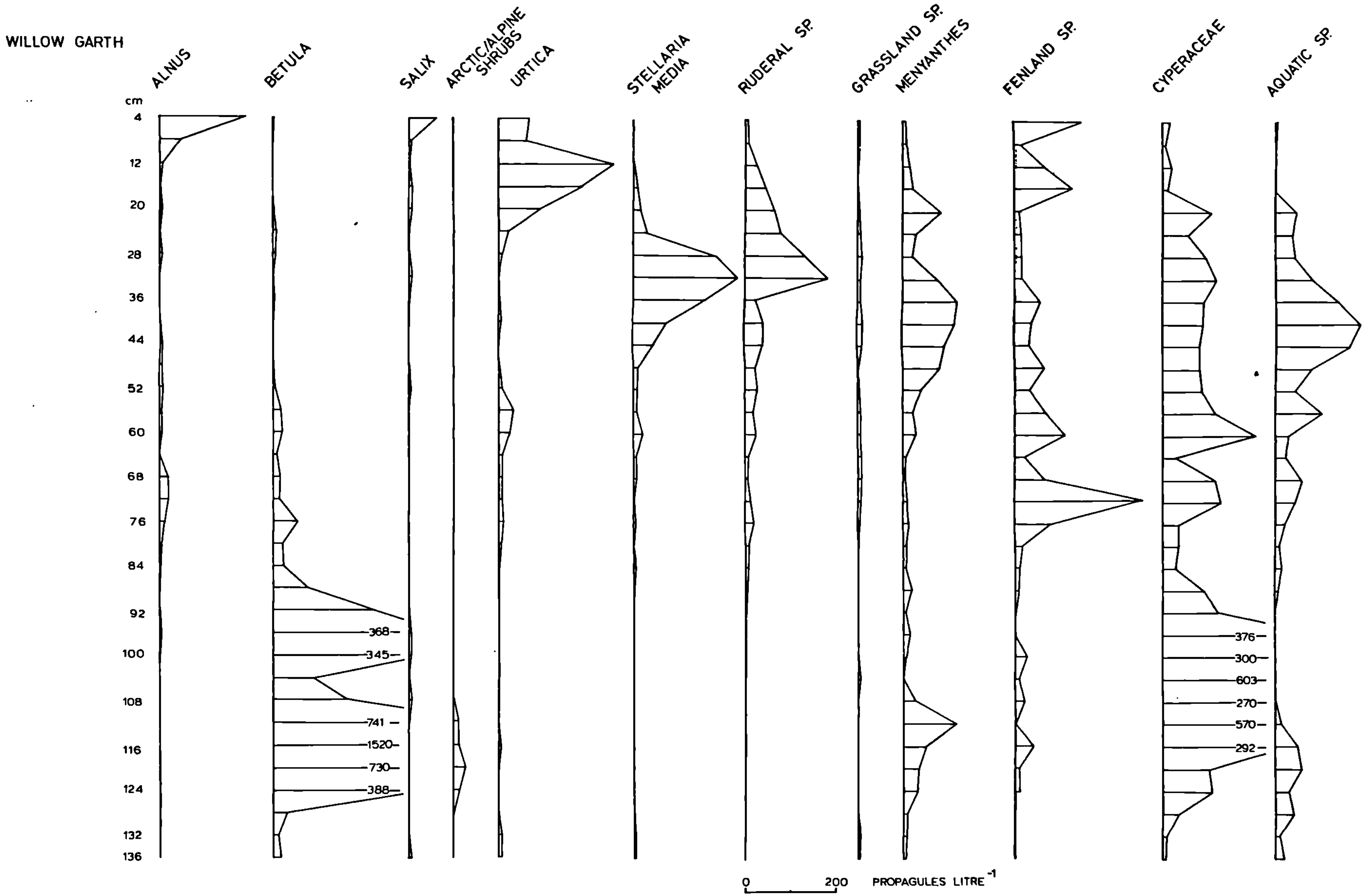


FIG. 7.7 CONCENTRATION OF PLANT PROPAGULES OF SELECTED TAXA AT WILLOW GARTH

also present. Tree Birch was highest in the basal sample of this zone attaining 41.7% of the total propagule count. This decreased to 23% in the sample above and finished at 29%. Betula nana, Salix, Stellaria and Urtica dioica were present in the basal sample. At 132 cm the sample contained Gramineae (Poaceae), Papaver, Lychnis alpina, Stellaria, U. dioica and Saxifraga. Other macrofossils from these levels included timber of Alnus, bud scales of Salix and leaves possibly of Salix repens. The sample at 128 cm was rich in Chara oospores; more than a thousand was the estimated number. This represented the densest concentration of these propagules found in the deposit.

WGS-2 (124 - 113 cm)

The concentration of fruits was considerably higher, 650 to 2044 fruits per litre. The diversity of species was constant at 12 or 13 taxa in each level.

An increase in tree birch characterised this level; Betula increased from 60% in the basal level of this zone to c. 75% in the other samples. Betula, Potamogeton praelongus agg. (2% to 11%), Menyanthes (3% to 4%) and Arctostaphylos (1% to 2%) are present in all levels. Betula nana fruits were found at 120 cm and fruits of Empetrum nigrum were present in the levels at 116 and 120 cm. Sonchus palustris, Cladium mariscus and Rosa were also present in this zone. The same obligate aquatics are present as in the previous level, except that Callitriche was replaced by Groenlandia densa, and they represented 2% to 16% of the total (48 to 102 fruits per litre).

Alnus timber was again present and Betula bud and catkin scales (B. pubescens) were abundant. Remains of B. nana were found at 120 cm. These were: catkin scales, a portion of a female catkin still containing fruits, and two identifiable leaf fragments. Populus and Salix bud scales were also present. Eighty to 250 Chara oospores were recorded in each level (c. 200 to 500 oospores per litre).

WGS-3 (112 - 85 cm)

The concentration of propagules diminished throughout this zone from 1623 to 356 fruits per litre. Species diversity was consistently low with most levels containing 7 taxa; the maximum, in the uppermost level was 11.

Betula fruits dominated with a peak of 74.4%. At 104 cm Carex spp. doubled their concentration and depressed Betula to 13.6%. There was a reduction in the number of fruits of obligate aquatics throughout this zone, and none was recorded between 108 and 92 cm. At 88 cm Sparganium and Potamogeton polygonifolius agg. were present. Throughout the zone the fen taxa, e.g. Carex cf. riparia, Carex cf. panicea, Pedicularis palustris and Menyanthes, expanded. Arctostaphylos and Empetrum nigrum were lost from the record after 112 cm. An Alnus fruit was recorded from 96 cm and Salix capsules were present in three levels. At 88 cm the herbs Ajuga reptans, Ranunculus sec Ranunculus and Potentilla reptans were recorded for the first time.

Other plant macrofossils included many tree-birch female catkin scales, bud scales and a complete, well-preserved leaf of Betula pubescens at 100 cm. Chara oospores were present in most samples but absent between 104 and 112 cm and again at 92 cm.

WGS-4 (84 - 77 cm)

Propagule concentration was very low at *c.* 93 fruits per litre but species diversity was greatly increased with 22 taxa recorded from 80 cm.

Betula fruits were less dominant in this assemblage with 22% (19 to 22 fruits per litre). Cyperaceae represented 30% to 35% of the total. New taxa were *Hydrocotyle vulgaris*, *Eleocharis* and *Filipendula ulmaria* from the fen flora. *Aphanes arvensis*, *Stellaria media* and *Chenopodium album* were also present totalling 3%. Obligate aquatic species were more plentiful than in the preceding zone: *Ranunculus flammula*, *R.* sec *Batrachium*, *R. sceleratus*, *Potamogeton* spp. and *Sparganium* totalled 8% to 15%. *Alnus* fruits were present in both levels at *c.* 3%. *R.* sec *Ranunculus* and *Urtica dioica* were both abundant totalling *c.* 11%.

Other plant macrofossils included timber of *Salix* and *Alnus*. The former was most abundant in these samples, and some of the pieces (stem wood) were 5 cm x 2 cm. *Betula* bud scales were present at 84 cm and in the same level a male *Alnus* catkin. At 80 cm a bud scale and leaf fragments of *Quercus* were recovered. *Chara* oospores were present in low numbers.

WGS-5 (76 - 69 cm)

Propagule concentration was higher in these two samples with 259 fruits per litre at 76 cm and 507 per litre at 72 cm. Species diversity continued to increase with 37 spp. per level.

Betula fruit concentration fell from 54 fruits per litre

(20%) to 13 (2%). An acorn was recovered from the uppermost sample, *Alnus* fruits maintained 3 to 4% of the total and *Arenaria* was recorded for the first time. *Aphanes arvensis*, *Moehringia trinervia*, *Polygonum aviculare*, *Chenopodium album* and *Atriplex* cf. *patula* totalled 3%. The increased diversity lay in the fen flora with the following recorded for the first time: *Hypochoeris*, *Eupatorium cannabinum*, *Caltha palustris*, *Lythrum salicaria*, *Berula erecta*, *Apium nodiflorum*, *Alisma plantago-aquatica* and *Bidens tripartita*. *Urtica dioica* reached a peak of 4% at 76 cm but declined to <1% at 72 cm.

A bud scale of *Alnus* and an anther of *Betula* were recovered from 76 cm and both levels yielded *Quercus* bud scales. *Quercus* timber was abundant at 76 cm. *Chara* oospores, scarce at 76 cm, were frequent at 72 cm.

WGS-6 (68 - 45 cm)

The propagule concentration in these samples was generally 300 to 400 fruits per litre. The species diversity increased from 24 at the base of the zone to a peak of 38 at 52 cm before dropping to 30 at 48 cm.

Cyperaceae (30% to 35%) remained the dominant component of this flora although other taxa have local peaks e.g. *Potentilla reptans* (12.5%), *Ranunculus* sec *Batrachium* (20%), *Urtica dioica* (7%) and *Menyanthes*, which gradually expanded to 23% at 48 cm.

The arboreal taxa were poorly represented with a single acorn at 68 cm, a hazelnut and a haw at 60 cm and birch reduced to 4% and actually disappearing from the record at 48 cm. Fruits of Alnus occurred in three levels. The fen flora continued to expand with fruits of Thalictrum flavum, Lycopus europaeus, Stellaria alsine and Juncus articulatus appearing for the first time. Ajuga reptans, present in every sample, attained 7% at 64 cm. Excluding the Cyperaceae the fen flora accounted for 40 to 50% of the total fruit sum during this zone. Polygonum persicaria, P. lapathifolium, P. aviculare, Raphanus raphanistrum, Stellaria media, Anagallis arvensis and Anthemis cotula were present in low numbers totalling c. 9%. Gramineae, Linum catharticum, Hypericum and Prunella vulgaris were also present in most of the samples of this zone. The obligate aquatic flora attained values of 22.5% as Myriophyllum, Oenanthe and Baldellia ranunculoides occurred for the first time.

Other plant macrofossils were scarce, with a Populus bud scale at 52 cm and a Salix bud scale at 48 cm. Chara oospores were recorded in all levels, ranging from scarce (<20) to abundant (>300) at 48 cm.

WGS-7 (44 - 29 cm)

The fruit concentration of this zone increased from 475 to 712 fruits per litre. The wetland flora was much reduced which was reflected in a decline in species diversity from 38 taxa at 40 cm to 19 at 32 cm.

The zone was characterised by a peak of weeds of disturbed ground e.g. Stellaria media (32.6%), Atriplex (12.5%) and Chenopodium album which together total 58% in the uppermost level. Papaver rhoeas, Euphorbia exigua, Rorippa islandica, Scleranthus annuus and Fumaria officinalis occurred for the first time. The obligate aquatic flora had a peak of 34% at the base of the zone but declined thereafter. Matching this was a decline in the fen flora from 25 to 14%. *Isolepis setacea*, *Nasturtium microphyllum*, *Valeriana officinalis* and *Valerianella dentata* occurred briefly before the decline of fen vegetation at *c.* 40 cm.

No other plant macrofossils were recorded with the exception of *Chara* oospores which were present in low numbers until 36 cm.

WGS-8 (28 - 21 cm)

Propagule concentration declined to 282 fruits per litre, but species diversity was constant at *c.* 27 spp..

Stellaria media (29.5%) and *Chenopodium album* (18.9%) at the base of the zone give way to *Urtica dioica* which starts to increase at 24 cm. Disturbed ground taxa represented 51% of the basal assemblage but were reduced to 29% at 24 cm. Obligate aquatics, *Menyanthes* and the other fen species continued the decline which had started in the previous zone. Arboreal taxa were scarce.

25 *Chara* oospores were recorded from the sample at 24 cm.

WGS-9 (20 - 17 cm)

The propagule concentration of this level was 384 per litre representing 19 taxa.

This zone was characterised by an increase in *Menyanthes* (18.5%), the continued increase of *Urtica dioica* (21%) and the decline of *Stellaria media* (3%). The representation of weeds of disturbed ground fell to 13%. *Alnus* (1%) and *Salix* (1.5%) were both present in this level.

50 *Chara* oospores (*c.* 150 per litre) were found in this sample.

WGS-10 (16 - 9 cm)

Fruit concentration was constant at *c.* 450 fruits per litre but species diversity was low with *c.* 12 to 13 taxa.

A peak of *Scrophularia* (26.5%) and *Urtica dioica* (55%) characterised this assemblage. *Alnus* (<1%) and low Cyperaceae (2 to 4%) distinguished this zone from the one above. The fen flora was reduced with *Juncus conglomeratus* agg., *Scrophularia* and *Menyanthes* totalling *c.* 18 to 28% of the assemblage. *Silene dioica* (12%) was abundant at 12 cm. The weeds of disturbed ground, excluding *U. dioica*, were also much reduced at 8 to 10%.

No *Chara* oospores were recorded.

WGS-11 (8 - 0 cm)

Propagule concentration varied between 137 and 496 fruits per litre and species diversity ranged from 16 to 19 taxa.

Four taxa formed peaks in this zone: *Alnus* (39%), *Urtica* (43%), *Salix* (12%) and *Filipendula ulmaria* (22.6%). The fen flora was represented by *F. ulmaria*, *Lychnis flos-cuculi*, *Iris pseudacorus*, *Caltha palustris*, *Menyanthes trifoliata* and *Angelica sylvatica*. Disturbed ground weeds, *Chenopodium album*, *Atriplex*, *Rumex* and *Euphorbia exigua* were present totalling 3%. Obligate aquatics were absent above 8 cm but single fruits of *Alisma* *plantago-aquatica* and *Ranunculus* sec *Batrachium* were recovered from the surface sample.

Macrofossil remains included the leaves and bud scales of the overhanging trees, which were *Salix* and *Populus*, and the rhizomes of *Iris pseudacorus*. No *Chara* oospores were recorded.

7.6.3 Mollusc Stratigraphy

WGM-1 (136 - 124 cm)

The concentration of shells in this level was low with 8 to 80 shells per litre. 11 species were recorded from this zone.

The obligate aquatic taxa dominated the zone, 6 of the species present were *Pisidium* spp.. These included *P. lilljeborgi* and *P. pseudosphaerium* (Fig. 7.9). Other aquatic taxa included *Gyraulus acronicus*, *Ovatella myosotis* and *Anisus leucostoma*. Also present was the waterside species *Succinea putris*, and the hygrophile *Cochlicopa lubrica*.

There were insufficient shell remains for statistical analysis between 120 cm and 44 cm.

WGM-2 (44 - 25 cm)

Shell concentrations in this zone increased from 60 to 380 shells per litre. The diversity of taxa also increased from 12 to 16 taxa.

Obligate aquatic taxa were again the dominant group, although there were fewer *Pisidium* than in WGM-1. Other taxa had colonised the pools. These included: *Bathyomphalus contortus*,

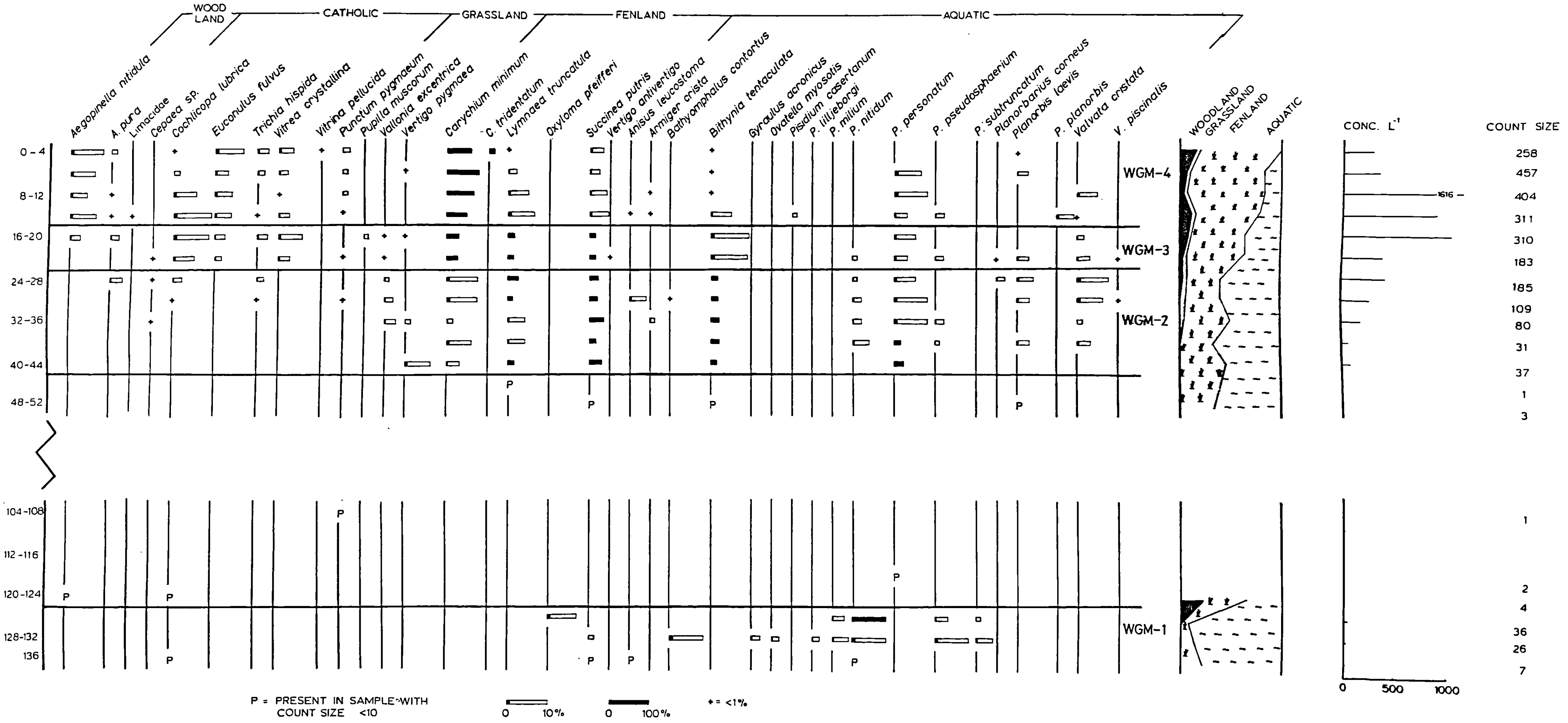


FIG. 7.9 PERCENTAGE MOLLUSC DIAGRAM FROM FOSSIL DEPOSITS AT WILLOW GARTH. POLZON ZONES INDICATED

Planorbis spp., Valvata piscinalis, V. cristata, Bithynia tentaculata and Anisus leucostoma. This group accounted for 52% to 68% of the assemblage. Waterside species were also abundant with such taxa as: Lymnaea peregra and Succinea putris. These accounted for a further 30% of the total. Carychium minimum was present in each sample at <3% and Vallonia excentrica was first recorded at 36 cm.

WGM-3 (24 - 17 cm)

Mollusc concentrations increased to 900 shells per litre at 20 cm. 17 species were recorded from this level.

High values of Lymnaea truncatula (30%) and Carychium minimum (33%) characterised this zone. The obligate aquatic taxa were reduced to 31.3% whilst the fen fauna increased to 45% and included Vertigo antivertigo and V. pygmaea for the first time. Dry land species such as Trichia hispida, Euconulus fulvus and Cochlicopa lubrica increased to 17% and Aegopinella nitidula increased from 1% to 5%. Vallonia excentrica and Pupilla muscorum were present at c. 1%.

WGM-4 (16 - 0 cm)

Mollusc concentration in these levels ranged from 200 to 1600 shells per litre, and there was the maximum species diversity of any level, 19 taxa, at 16 cm.

Fen species increased in dominance from 57% to 78% and obligate aquatics diminished to 2%. Carychium minimum was the dominant taxon of this zone with up to 74% of the total count. Catholic dry land species diminished from 17% to 8% whilst woodland taxa increased to 6%. Species of open ground were virtually absent, with a single occurrence of Vertigo pygmaea at 8 cm.

7.6.4 Gramineae Size Data Stratigraphy

WGG-1 (136 - 132 cm)

A small range of pollen sizes from 22 to 35 µm, with a modal peak at 24 to 25 µm characterised this zone. The size category from 22 to 23 µm was well represented with 20 grains (16%) (Fig. 7.10).

WGG-2 (132 - 107 cm)

A wider range of size-classes were represented in this zone. In the lower samples there was a modal peak at 26 to 27 µm (34%) and 30 to 31 µm (32%). The level was characterised by an overall increase in pollen sizes with some as large as 52 µm. The size distribution became highly postively skewed as the larger categories declined and a new modal group at 24 to 25 µm (30%) emerged.

WGG-3 (106 - 69 cm)

This zone is characterised by the modal group at 24 to 25 µm. In just one sample this peak is transfered to the 26 to 27 µm size class. The general range of sizes was from 20 to 34 µm, forming a similar assemblage to WGG-1. In four consecutive samples from 87 to 93 cm there was an extended range of sizes of up to 52 µm. In the upper samples of this zone there is an

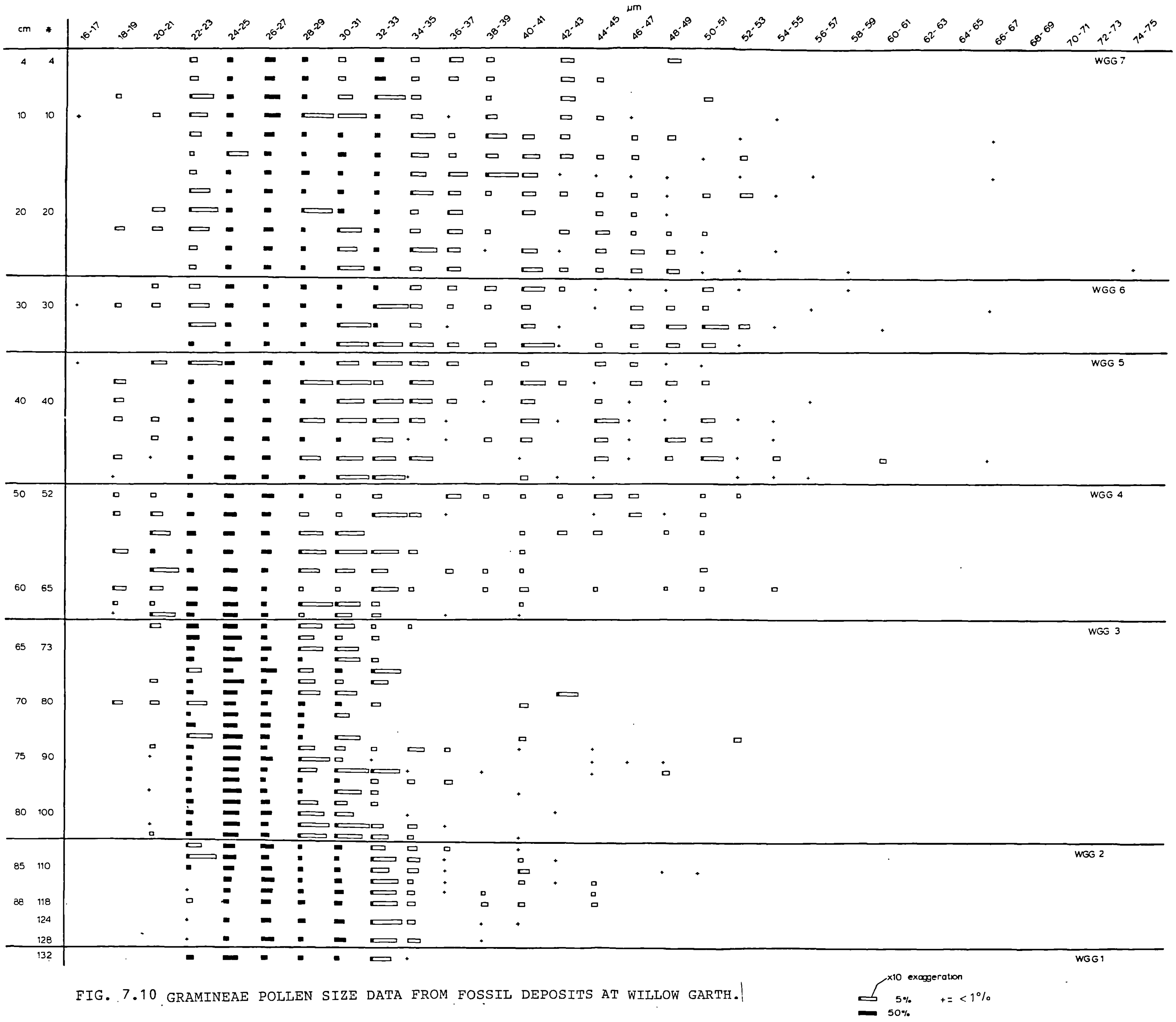


FIG. 7.10 GRAMINEAE POLLEN SIZE DATA FROM FOSSIL DEPOSITS AT WILLOW GARTH.

increase in theabundance of the size classes 22 to 23 µm (12 to 30%) at the expense of the 26 to 27 µm size class which falls correspondingly.

WGG-4 (68 - 52 cm)

This zone was characterised by an expansion of the size classes so that the overall range is 18 to 56 µm. These include the first definite identifications of Cerealia pollen and there is up to 10% of the grass pollen total exceeding 44 µm in size. The modal peak was spread between 22 and 27 µm (*c.* 70%) with a slight increase in the 26 to 27 µm category at the top of the zone.

WGG-5 (48 - 36 cm)

The trend towards increasing sizes was continued in this zone with a maximum of 66 µm. As much as 19% of the grass pollen total exceeded 44 µm. The modal peak was unaltered at 24 to 27 µm, although the percentage contained within that peak (40%) was less.

WGG-6 (34 - 28 cm)

During this zone the modal peak was spread across a size range from 24 to 33 µm accounting for 63% of the total. Cerealia pollen is present and the large sized Gramineae pollen reached a peak of 21%.

WGG-7 (26 - 8 cm)

The size category 30 to 31 µm reached a peak at 16 cm (20%)

and then diminished to 2%. Cerealia were present and the largest (74 to 76 µm) were probably Secale cereale .

WGG-8 (8 - 0 cm)

Characterised by a bimodal peak at 26 to 27 µm and 32 to 33 µm, Cerealia were infrequent from this zone.

7.7 THE TWINSPAN CLASSIFICATION OF FOSSIL GRAMINEAE POLLEN SIZE DATA

The TWINSPAN analysis produced the dendrogram shown in Fig. 7.11. It may be seen from this figure that the first division separated the upper section of the core into a negative group (0) which also contained the sample from 93 cm. The remainder was placed into the positive group (1). The sample from 91 cm was a misclassified positive and the sample from 8 cm a misclassified negative. This implies that the sample at 91 cm, like the neighbouring sample at 93 cm, showed a strong similarity to the groups from the open habitats in the post-clearance phases of the upper levels of the core. Similarly, the sample at 8 cm showed a likeness to those from the forested samples lower in the core.

The second divisive level defined a group from 108 to 112 cm and 114 to 132 cm which were placed in the group 11, separating these from the other samples in the lower part of the core. This group corresponds to the pollen zones WGP-2 and WGP-3, the arctic-alpine grassland zones. It is perhaps significant that in the other group (10) there has been placed, with the samples from the Betula forests, the sample from 136 cm.

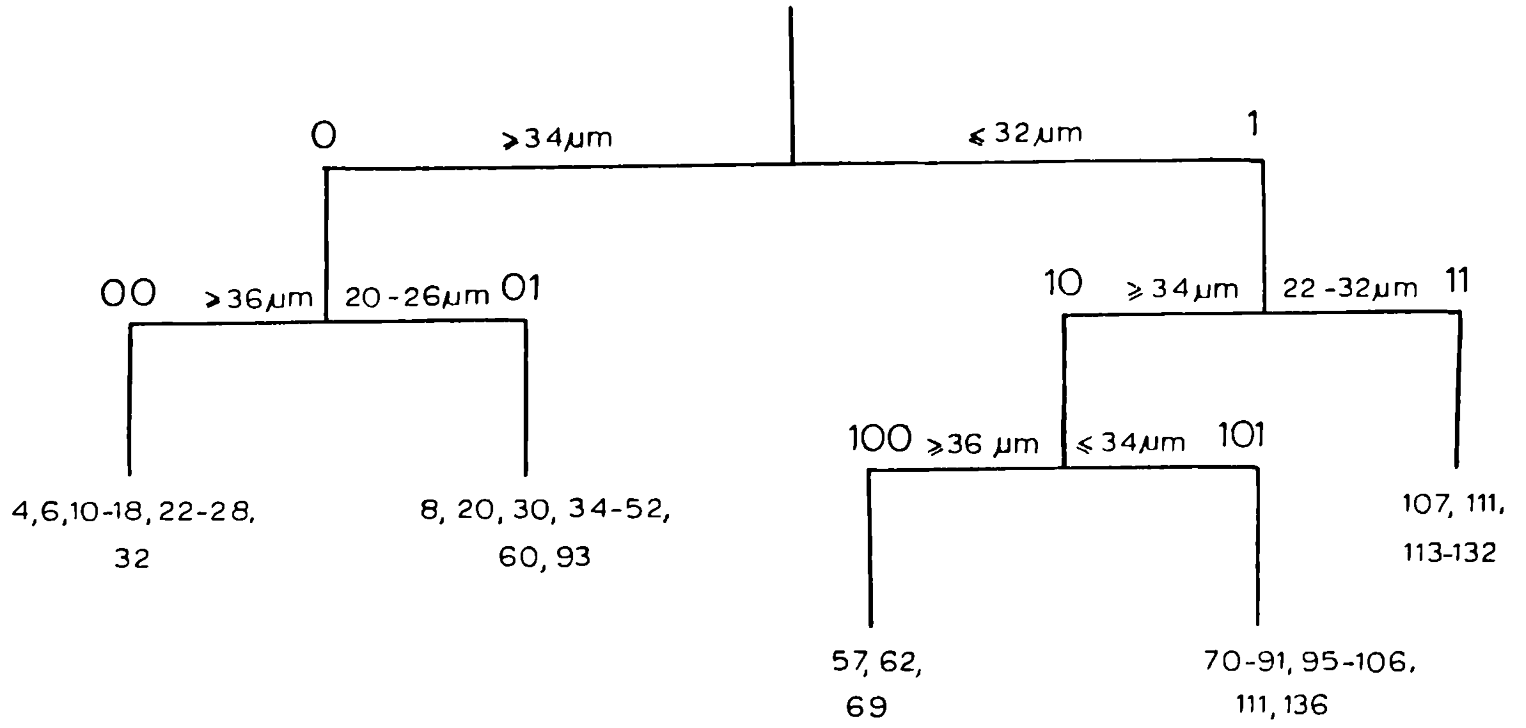


FIG. 7.11 RESULTS OF THE TWINSPAN ANALYSIS OF FOSSIL GRAMINEAE POLLEN SIZE DATA FROM WILLOW GARTH.

The third divisive level contained one division of note, that of group 10. Samples which were all from the *Betula*-forest period were placed in the positive group (101), whilst the temperate forests were separated into the negative group (100). The sample from 136 cm still lay with the *Betula*-forest dominated samples in the positive group.

7.8 ESTIMATED CANOPY COVER

The weighting values (R-rel) apply to a pollen source area of 20m radius around the point of deposition. To use these weightings on pollen production from more distant sources would be to ignore one of the constraints of the R-rel model (Bradshaw, 1981b). The deposit at Willow Garth covers a very small area. It is possible that arboreal taxa were present very close to the point of sediment accumulation, at least in the early post-glacial, before an extensive fen developed. If the woodland existed within 20 m of the site the pollen contribution from arboreal taxa might be expected to exceed 50%. However, as was shown in the study of modern pollen sites, if a woodland is relatively open, or immature, then the dominance of the arboreal component is reduced. As the Willow Garth currently has an open woodland cover, and the modern arboreal pollen yield of the site was *c.* 20%, this is the value set as the minimum threshold for the application of the pollen weightings. Although occasional levels near the top of the diagram exceeded 20% arboreal pollen the only consistent phases where there was this pollen proportion were in the pollen zones WGP-1 to WGP-6.

WGP-1

The downweighting of Betula and Pinus, and the positive weighting of Salix, suggested a value for Salix of 83% of the total arboreal canopy. Values for other taxa were: Corylus and Alnus (1%), Betula (11%) and Pinus (5%) (Fig. 7.12).

WGP-2

Only Pinus and Betula were present and as the weightings of these two are almost identical there was little change: Pinus (98%) and Betula (2%)

WGP-3

Pinus declined to 48% as other taxa, primarily Betula (30%) and Salix (20%) increased. Populus and Quercus were both present at <3%.

WGP-4

Betula increased to 90% of the canopy and Pinus was reduced to 8%. Salix, Populus, Ulmus and Corylus make up the other 2%. In the last sample of this zone Betula falls to 48% and Salix attains a brief peak of 43%.

WGP-5

Betula regained a dominance of the canopy (c. 82%) and at 78 cm reached a peak of 93%. Pinus attained a peak of 50% but was otherwise constant at c. 10% of the canopy. Quercus pollen became more abundant and attained a peak of 8%. Salix ranged between 10 and 16% and *Corylus* started to increase in abundance and attained a peak of 43% at the top of the zone. In the uppermost samples of the zone *Betula* declined from 80% to 30% and *Pinus* formed a new peak with as much as 63% of the canopy component. *Salix* declined to zero but *Alnus* increased to 8%.

WGP-6

Betula was reduced to less than 15% and *Pinus* declined to less than 1%. *Alnus* was the most abundant taxon (>50%). *Quercus* increased to 26% and the zone was marked by a peak of *Tilia*, which for three levels was in excess of 30% of the canopy. *Corylus* was abundant throughout this zone with values of up to 60% of the arboreal canopy.

7.9 THE DECORANA ORDINATION

7.9.1 Fossil Pollen Data

The result of the DECORANA analysis of the fossil pollen data set is shown in Fig. 7.13 in which the first two axes of the output were plotted. Axis 1 (Fig. 7.13), which had an eigenvalue of 0.512, places the open ground sites close to the origin, and at the positive extreme of this axis are the samples from the *Betula* forest. This would suggest that axis 1 represents an environmental gradient such as increasing shade. The second axis, which had an eigenvalue of 0.217, places the driest sites near the origin and the wettest sites at the positive extreme of the axis. This axis might therefore be interpreted as a gradient of increasing soil moisture.

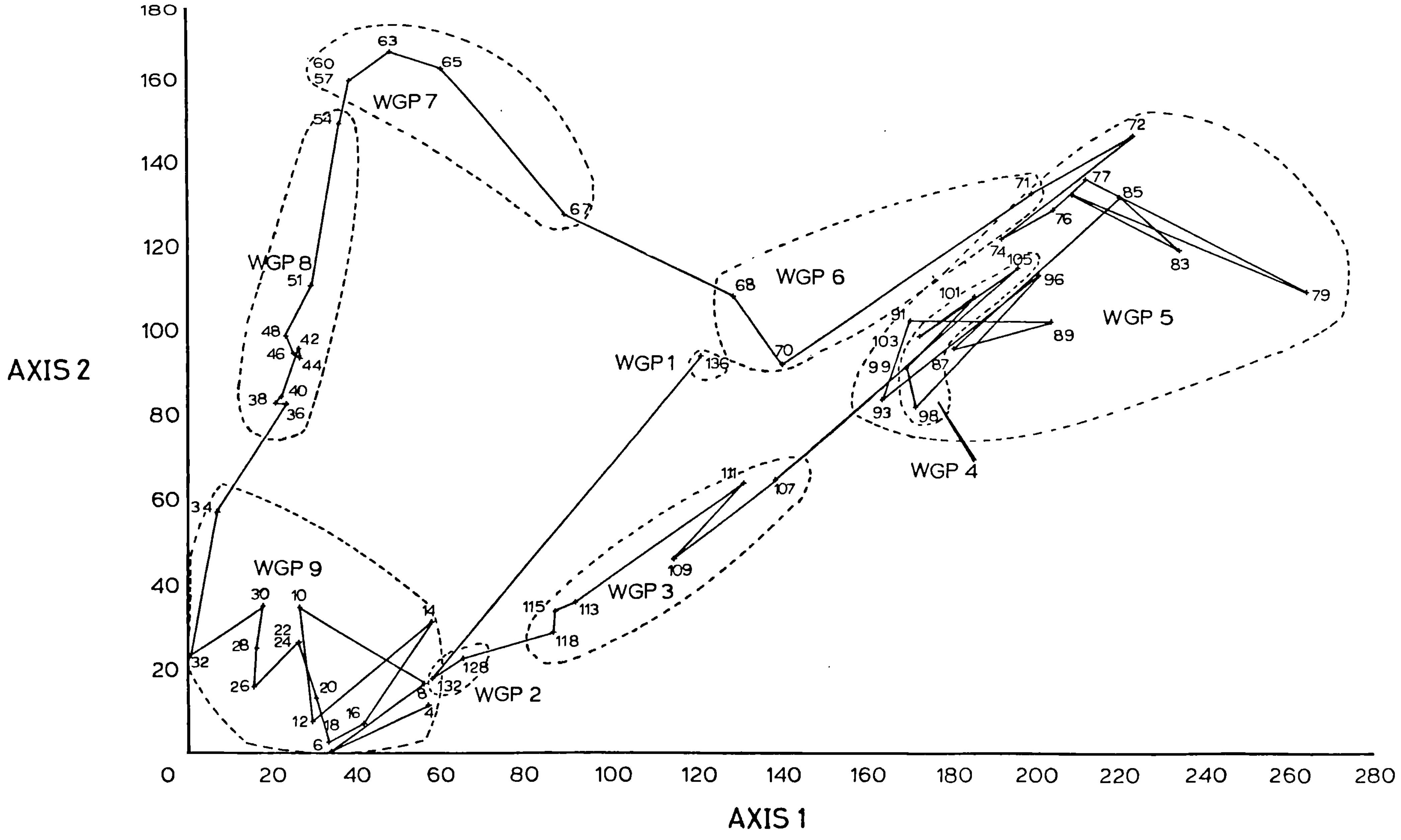


FIG. 7.13 RESULTS OF THE DECORANA ANALYSIS OF FOSSIL POLLEN DATA FROM WILLOW GARTH. BROKEN LINES INDICATE POLZON GROUPINGS

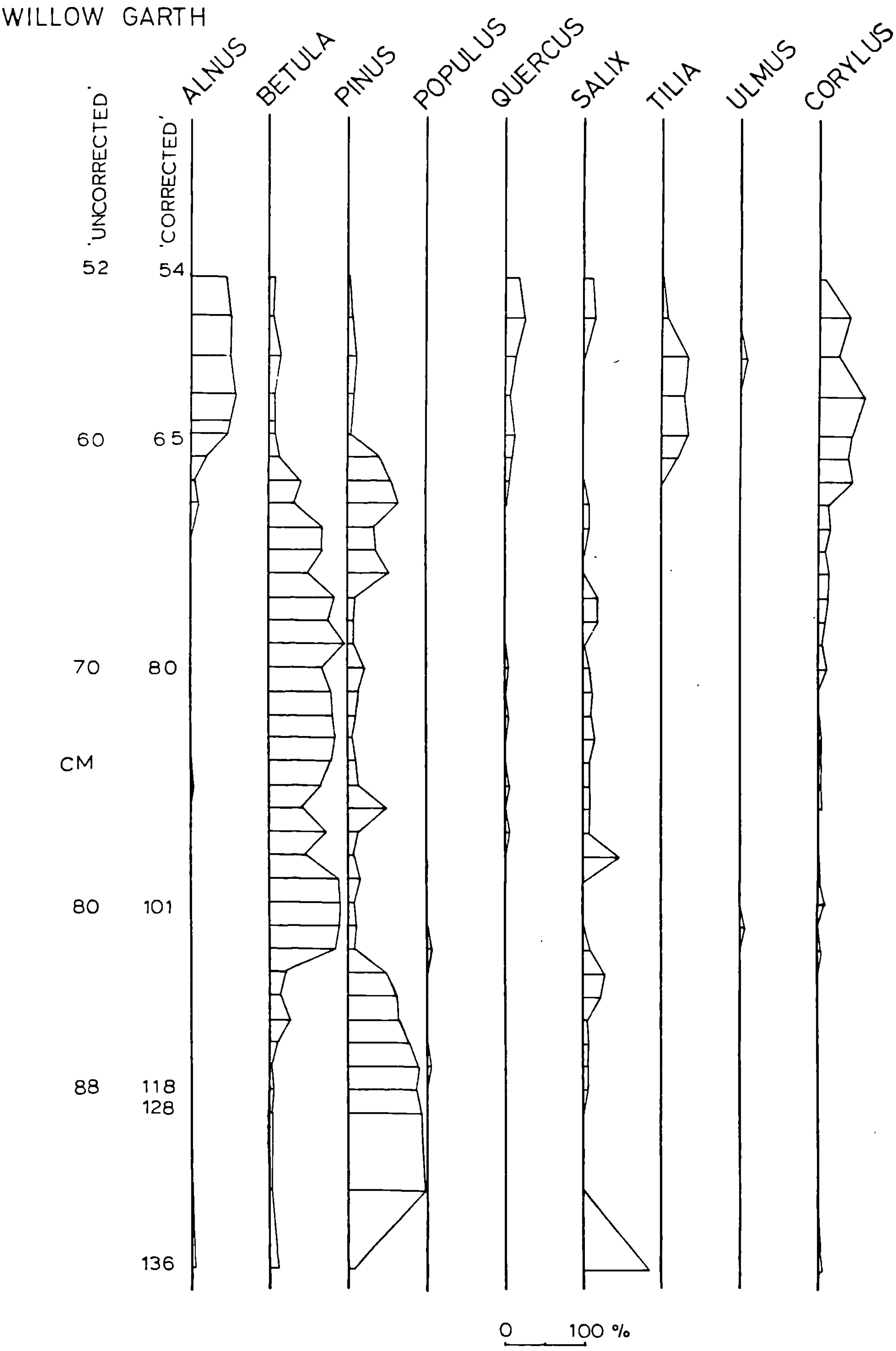


FIG. 7.12 WILLOW GARTH WOODLAND CANOPY COMPOSITION FROM 136 CM TO 56 CM. DERIVED FROM R-REL WEIGHTING OF POLLEN INFLUX DATA.

7.9.2 Fossil Propagules

The first axis defined by the DECORANA analysis had an eigenvalue of 0.705. This axis represented an environmental gradient from Betula dominated levels at the origin to those of the modern vegetation at the positive extreme. It would seem to be a feature of DECORANA that the first axis explains a massive amount of the variance within a data set. This results in the second and third axes being placed through the extremes of the first axis. This was the case in this analysis: the second axis spread the points which represented the dry woodland. As this is the modern woodland the four uppermost points were spread across an axis whilst all the wetland points were clustered in the middle of this axis. This was of little use for the present study and so the second axis was discarded. The third axis spread the points at the negative extreme of the first axis and as this was where the majority of the fossil data was grouped this was of considerably more value. This axis had an eigenvalue of 0.140 and placed the samples of WGS-1 at the positive extreme and the samples of WGS-5 at the negative extreme (Fig. 7.14).

The gradients on these axes would therefore appear to represent: axis 1 increasing shade and axis 3 decreasing temperature. However, without the use of modern analogues the environmental gradients represented are difficult to establish.

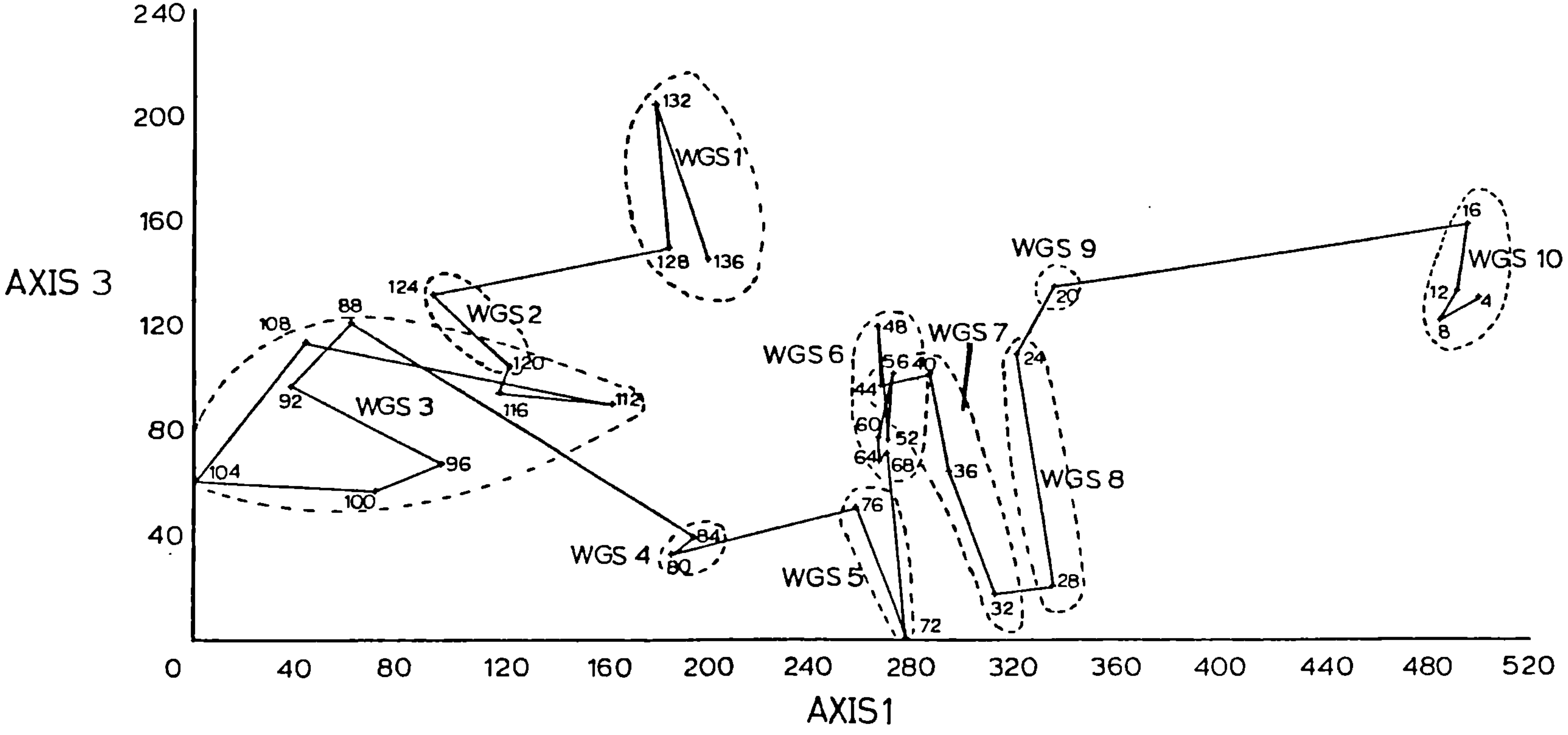


FIG. 7.14 RESULTS OF THE DECORANA ANALYSIS OF THE FOSSIL PROPAGULE DATA FROM WILLOW GARTH. BROKEN LINES INDICATE POLZON GROUPINGS.

7.10 COMPARISON OF MODERN AND FOSSIL SPECTRA

7.10.1 The Regional Trends: Pollen

The results obtained from the analysis of the modern and fossil pollen spectra are shown in Fig. 7.15 and the position for the mean value for each pollen zone is shown in Fig. 7.16. It is apparent from this latter figure that the majority of the pollen zones represented vegetation types without a modern counterpart on the Wolds. WGP-1, WGP-4, WGP-5, WGP-7 all lay outside the range of the modern analogue sites. Whilst WGP-2 and WGP-3 lay within the grassland group of modern pollen analogues, it was apparent from the species composition that there was a considerable climatic difference between the fossil and modern samples. Taxa such as Arctostaphylos, Empetrum, Saxifraga, Polygonum viviparum, Gentiana verna and Armeria maritima suggested a colder and/or drier environment. In order to extend the range of the analogues to encompass at least some of these samples it was necessary to utilise published data.

The data of Birks (1973) from the Isle of Skye combined a full vegetation survey with modern pollen rain analysis. Data from 6 of the samples listed by Birks were utilised. 4 of them were defined by Birks as Betula pubescens woodlands (labelled B 1 - 4) and two samples from the Agrosto-festucetum association of the sub-alpine grasslands (labelled B5 and B6) were also utilised.

With the inclusion of these points in the data set the orientation of the clusters was changed, although their relationship to each other, in other words their ecological distance, remained much the same (Fig. 7.17 and 7.18).

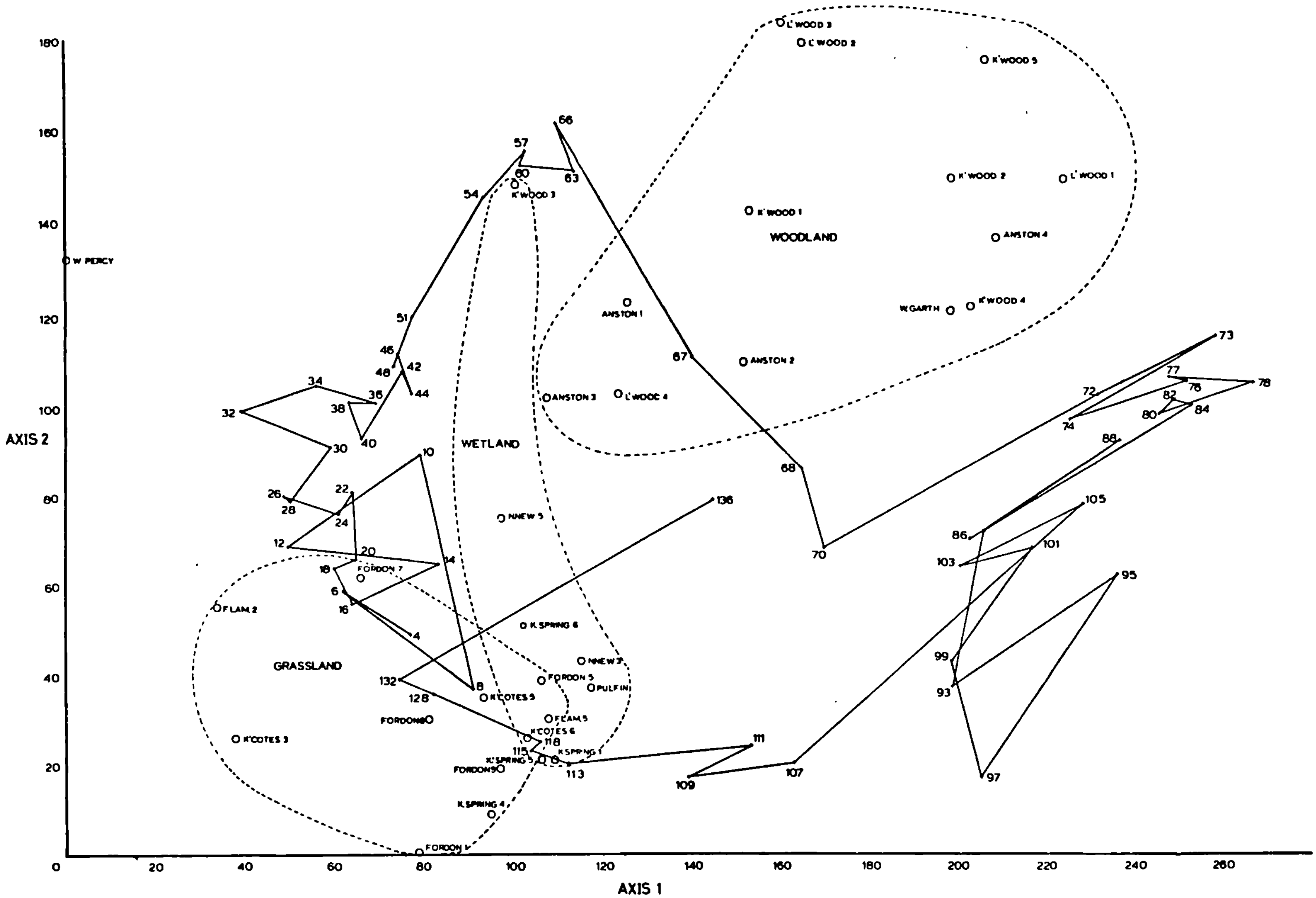


FIG. 7.15 RESULTS OF THE DECORANA ANALYSIS OF MODERN ANALOGUE AND FOSSIL POLLEN DATA FROM WILLOW GARTH. BROKEN LINES ENCLOSE TWINSPAN GROUPINGS OF ANALOGUE SITES.

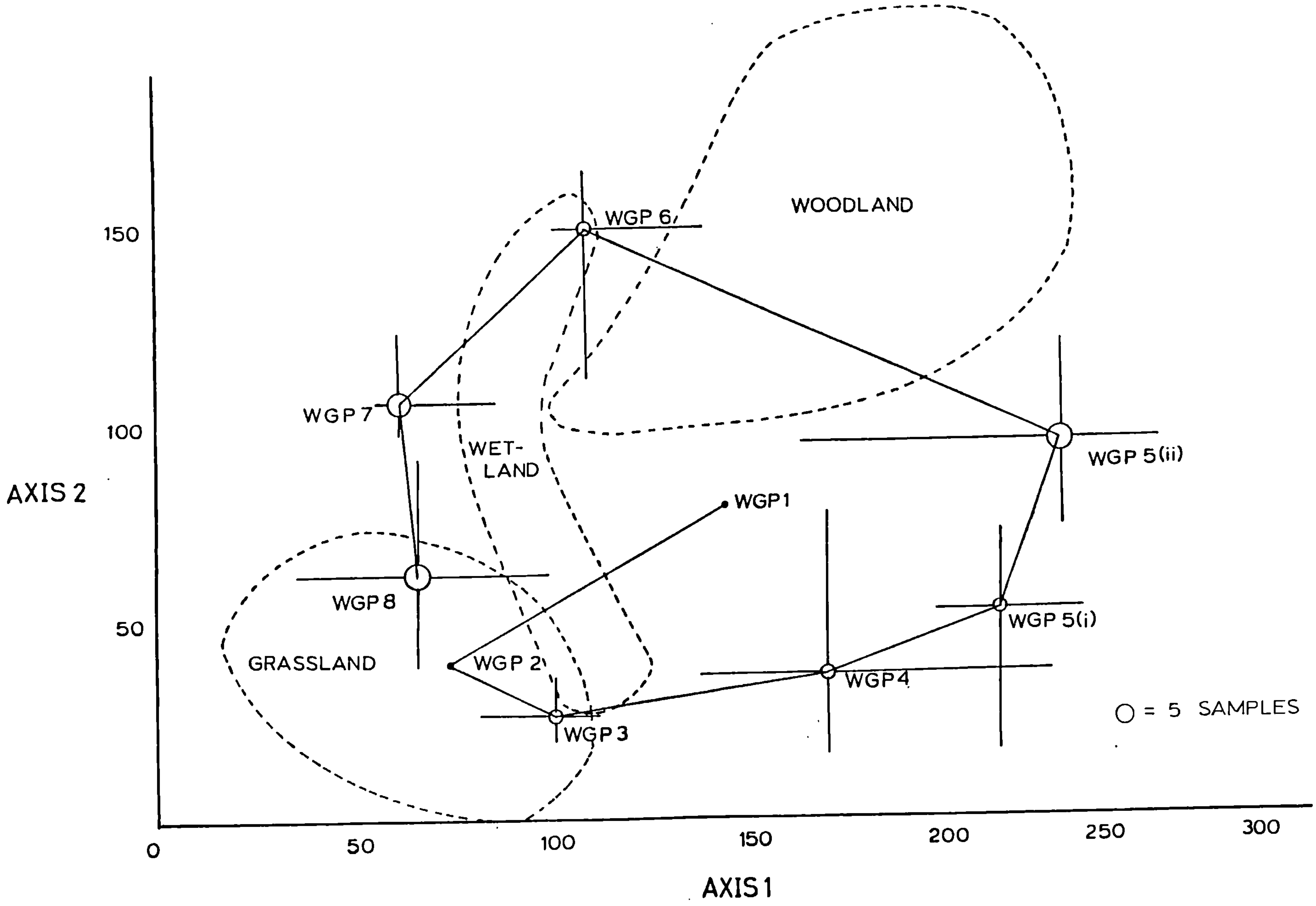


FIG. 7.16 SUMMARY DIAGRAM OF THE RESULTS OF THE DECORANA ANALYSIS OF MODERN ANALOGUE AND FOSSIL POLLEN DATA FROM WILLOW GARTH. BROKEN LINES INDICATE TWINSPAN GROUPINGS OF ANALOGUE SITES.

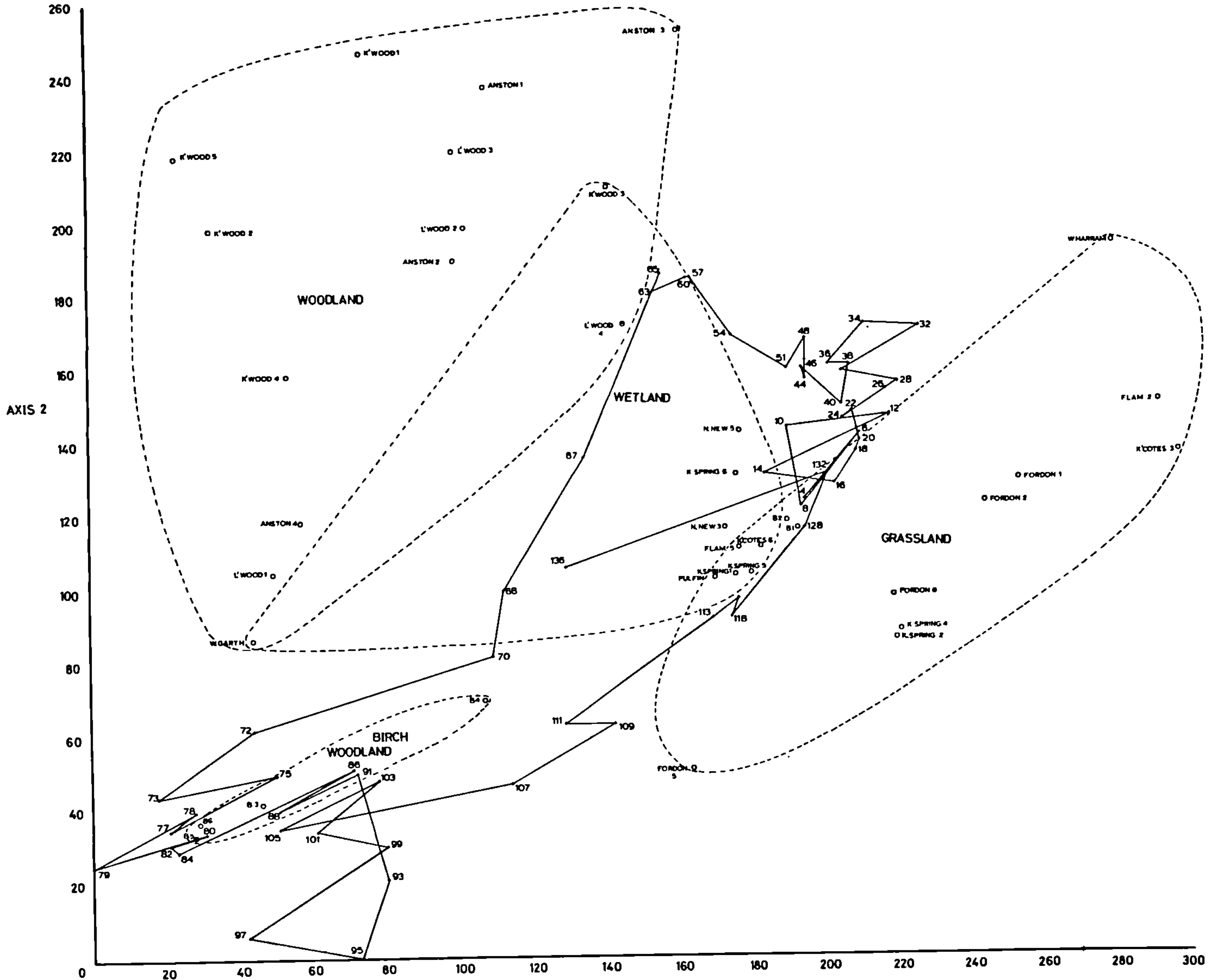


FIG. 7.17 RESULTS OF THE DECORANA ANALYSIS OF MODERN ANALOGUE AND FOSSIL POLLEN DATA FROM WILLOW GARTH PLUS SIX MODERN SAMPLES FROM THE ISLE OF SKYE. BROKEN LINES ENCLOSE TWINSPAN GROUPINGS OF ANALOGUE SITES

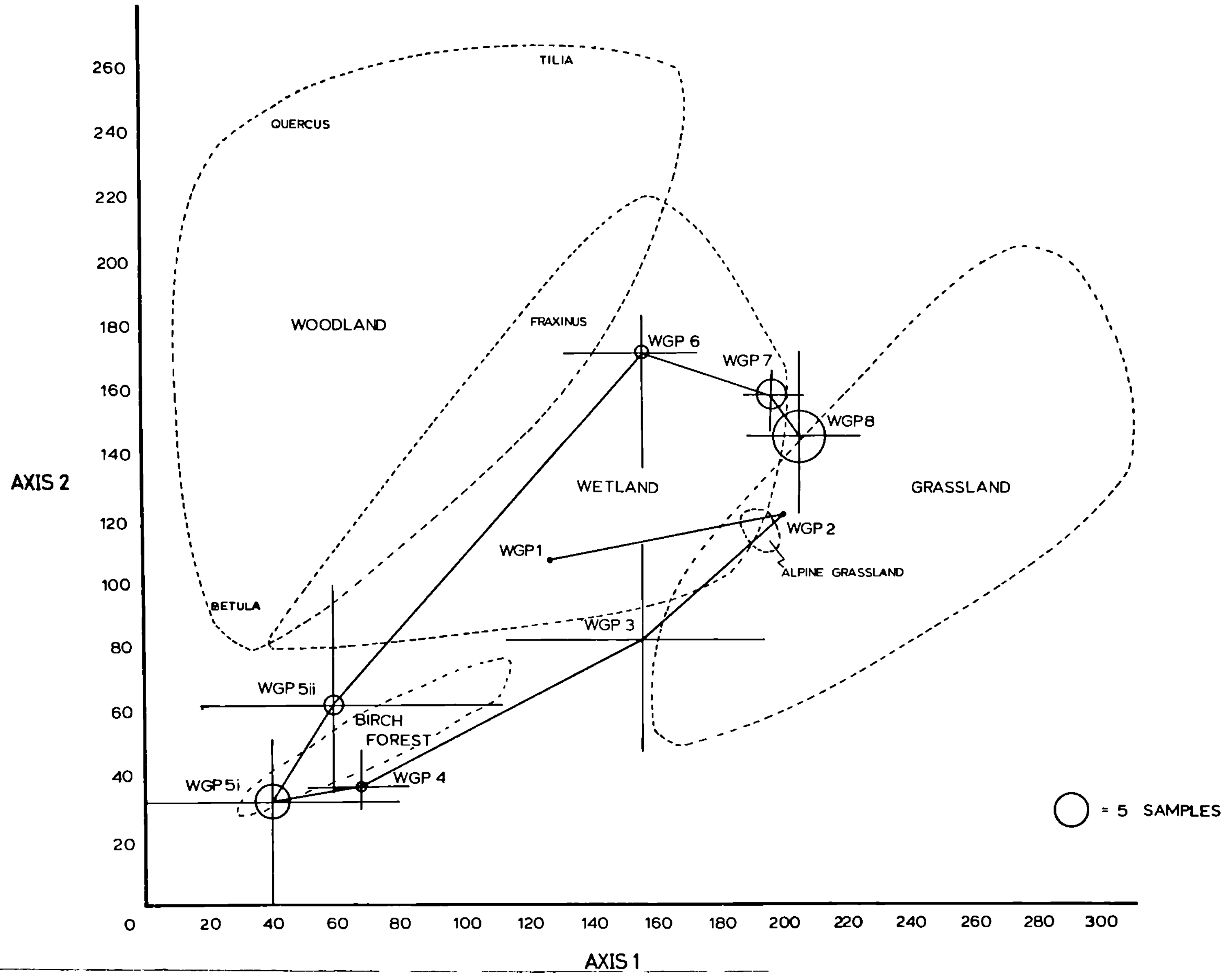


FIG. 7.18 SUMMARY DIAGRAM OF THE RESULTS OF THE DECORANA ANALYSIS OF MODERN ANALOGUE AND FOSSIL POLLEN DATA FROM WILLOW GARTH PLUS SIX MODERN SAMPLES FROM THE ISLE OF SKYE. BROKEN LINES ENCLOSE TWINSPAN GROUPINGS OF ANALOGUE SITES.

It can be seen from Fig. 7.17 that all the zones now lie within or close to modern analogue clusters. Axis 1 which has an eigenvalue of 0.499 would appear to be an environmental gradient of increasing light availability, whilst axis 2, with an eigenvalue of 0.389, leaves most of the open ground sites in a fairly central position and has separated the sites at the negative end of the first axis, the woodlands. At the negative extreme of this axis are the birch forests of Skye, and at the positive extreme the Tilia rich woodlands of South Yorkshire. This axis could therefore be one of decreasing rainfall, increasing temperature or decreasing soil acidity. Without more evidence it is not possible to be certain which it is. However, an edaphic factor would seem to be the most likely on the grounds that there is quite a wide separation within the Wolds woodlands which would probably experience similar temperatures and rainfalls.

Axes 3 and 4 were not readily interpretable.

The Betula pubescens forests recorded by Birks on Skye are clearly similar in their general composition to the forests represented by zones WGP-4 and 5. Birks records two types of Betula woodland, that associated with a tall herb community and that associated with Vaccinium myrtillus in the understorey. Samples B1 and B2 are from Betula with a tall herb understorey and B3 and B4 are from samples with Vaccinium myrtillus in the understorey. It may be seen from Fig. 7.18 that B1 and B2 represent the closest likeness to WGP-5 whereas neither B3 nor B4 are as close a match to any of the other fossil pollen zones.

Birks noted that although the pollen representation of understorey species was poor, pollen of tall herbs such as Filipendula ulmaria, Cirsium heterophyllum and Geum rivale was present in the tall herb understorey woodlands but absent from the V. myrtillus understorey woodlands. Fig. 7.3 shows that Filipendula, Epilobium, Cirsium and Potentilla (incl. Geum) were present in all the Betula dominated zones. This suggests that these taxa may not be solely indicative of fenland conditions, but could also have been growing in a relatively open birch woodland.

The general trends revealed in Fig. 7.17 are that WGP-1 (136 cm) is a wetland environment more closely related to the sample from 70 cm of WGP-5, and hence Betula pubescens woodlands, than to the grasslands of WGP-2. The trend from WGP-1 to WGP-2 is one from wet open woodlands towards a cold dry arctic-alpine grassland as indicated by the proximity of B5 and B6 to WGP-2. WGP-3 reflects the gradual transition from the extreme of WGP-2 towards the Betula-rich samples of WGP-4 and WGP-5. Group WGP-5 represents a zone in which there are considerable fluctuations in the occurrence of Betula pollen. In the upper samples of this group there is a trend towards less Betula, and more Quercus and Corylus pollen. Group WGP-6 lies within the wetland zone, showing a considerable affinity with the wet forest site of Kingswood 3 and the regenerating woodland site of Littlewood 4. Groups WGP-7 and WGP-8 demonstrate a progressive shift away from a woodland environment, through the wettest analogue sites and on towards the drier grasslands and fen meadows.

7.10.2 The Local Trends: Macrofossils

The DECORANA analysis of the combined data matrix of modern and fossil propagule samples produced a first axis with an eigenvalue of 0.825 which represents increasing light availability with the woodland sites clustered near the origin of axis one and the unshaded sites of Flamborough and Fordon Chalk Bank at the opposite extreme. The second axis separated the modern analogue grassland group without affecting the fossil data, leaving the fossil sites grouped in a narrow band in the middle of axis 2. Axis 3 which had an eigenvalue of 0.471 separated the wetland communities. The wooded fen carrs of Kingswood 3, Kiplingcotes Spring 6 and Willow Garth were at the origin of this axis whilst the more diverse fen meadows of North Newbold were at the positive extreme. As most of the fossil samples had a major wetland component this axis was utilised in preference to axis 2 (Figs. 7.19 and 7.20).

The molluscan assemblages were missing from the peat sections of the core; only 13 samples contained sufficient numbers of shells for statistical analysis. The first axis of the DECORANA analysis of the combined fossil and modern data sets, which had an eigenvalue of 0.626, represents an environmental gradient of increasing soil wetness, with the relatively arid sites of chalk grassland at the origin and the open water sites of Leven Canal and Brandesburton Gravel-Pit at the positive extreme. The second axis, with an eigenvalue of 0.158, which is

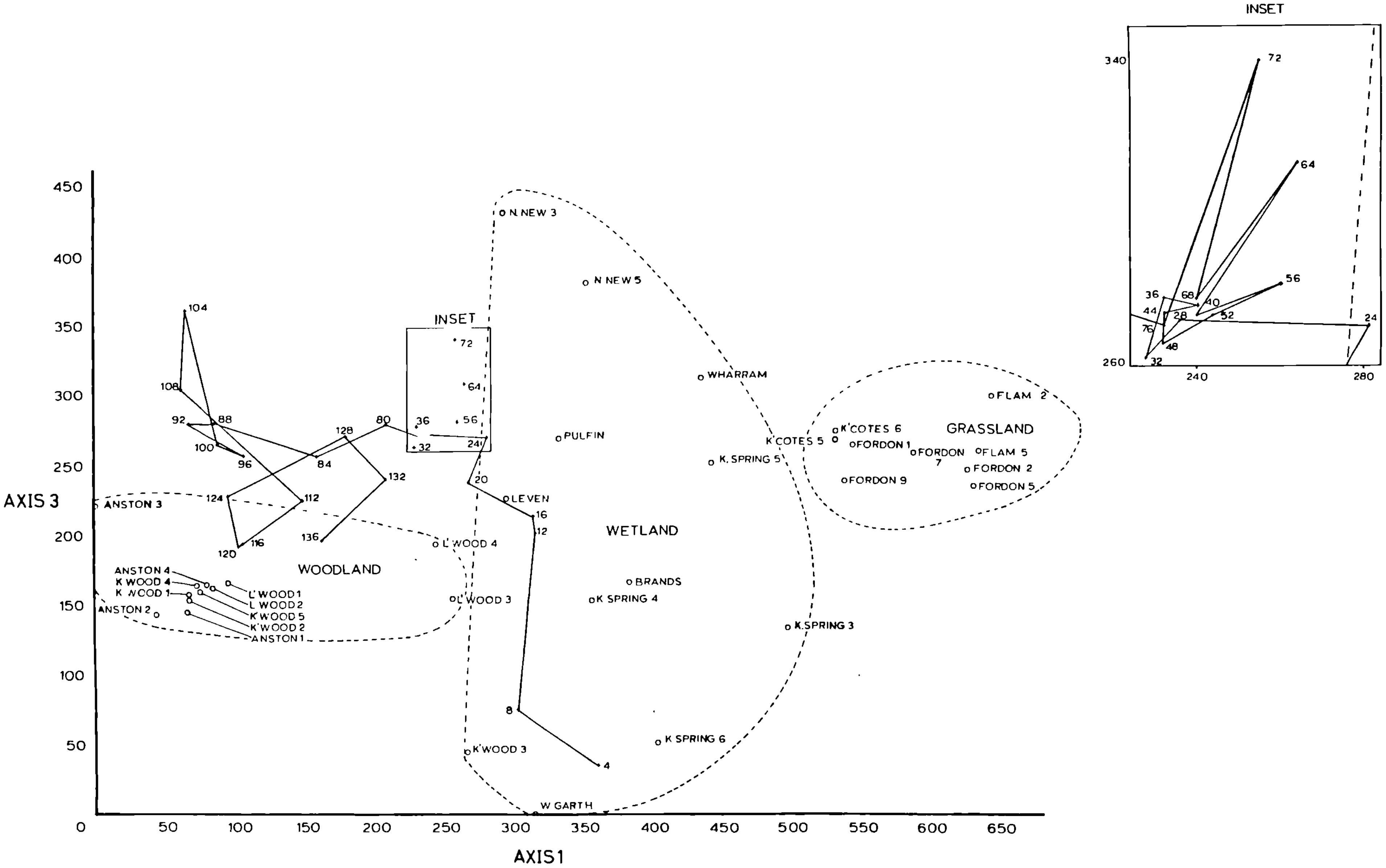


FIG. 7.19 RESULTS OF THE DECORANA ANALYSIS OF MODERN ANALOGUE AND FOSSIL PLANT PROPAGULE DATA FROM WILLOW GARTH. BROKEN LINES ENCLOSE TWINSPAN GROUPINGS OF ANALOGUE SITES.

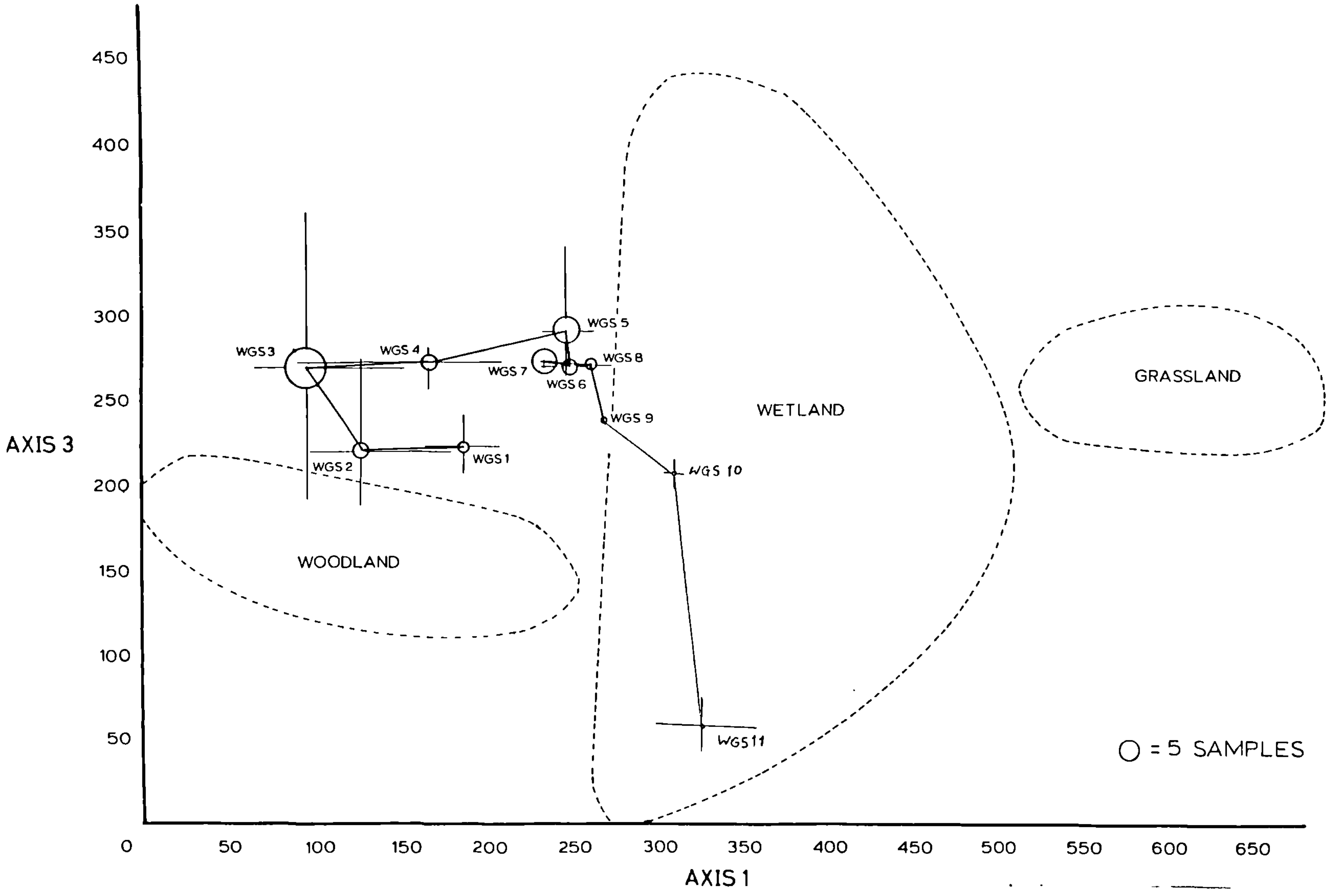


FIG. 7.20 SUMMARY DIAGRAM OF THE RESULTS OF THE DECORANA ANALYSIS OF MODERN ANALOGUE AND FOSSIL PLANT PROPAGULE DATA FROM WILLOW GARTH. BROKEN LINES ENCLOSE TWINSPAN GROUPINGS OF ANALOGUE SITES.

probably of increasing light availability, has Flamborough 2 at the origin of the axis with the sites of Anston Stones Wood and Kingswood, whilst at the positive extreme are the sites of Fordon Chalk Bank (Fig. 7.21). It is surprising to find Flamborough 2 associated with the woodlands but perhaps the north-facing aspect of this site and the damp sea air affects the microclimate in which the molluscs live, creating an environment very different from the south facing slopes of Fordon Chalk Bank and more similar to a dank woodland floor.

The cluster WGM-1 corresponds stratigraphically with the fossil propagule cluster at WGS-1 and the earliest level of WGS-2. The mollusc data is firmly within the wetland zone of the DECORANA analysis although there is some trend towards a drier environment (Fig. 7.21). During the corresponding period the propagule assemblage indicates a forest retreat between 136 and 132 cm to an environment in WGS-2 and WGS-3 which has no modern analogue on the Wolds (Fig. 7.20). The relative position of these two sites suggests a gradual increase in fen diversity and the return of a woodland component. Zone WGS-4 again lies outside the range of modern analogues but there has been a marked move away from the woodland influence. This trend continues in the next four zones. Between WGS-8 and WGS-9 there is a change in the fen flora towards a wet wooded, alder carr environment. WGS-9, the most recent zone, is the first to lie within a modern analogue group.

The mollusc data which restarts at 44 cm has a characteristic wetland assemblage at that point but at 36 cm there starts a progressive drying of the fen environment. The

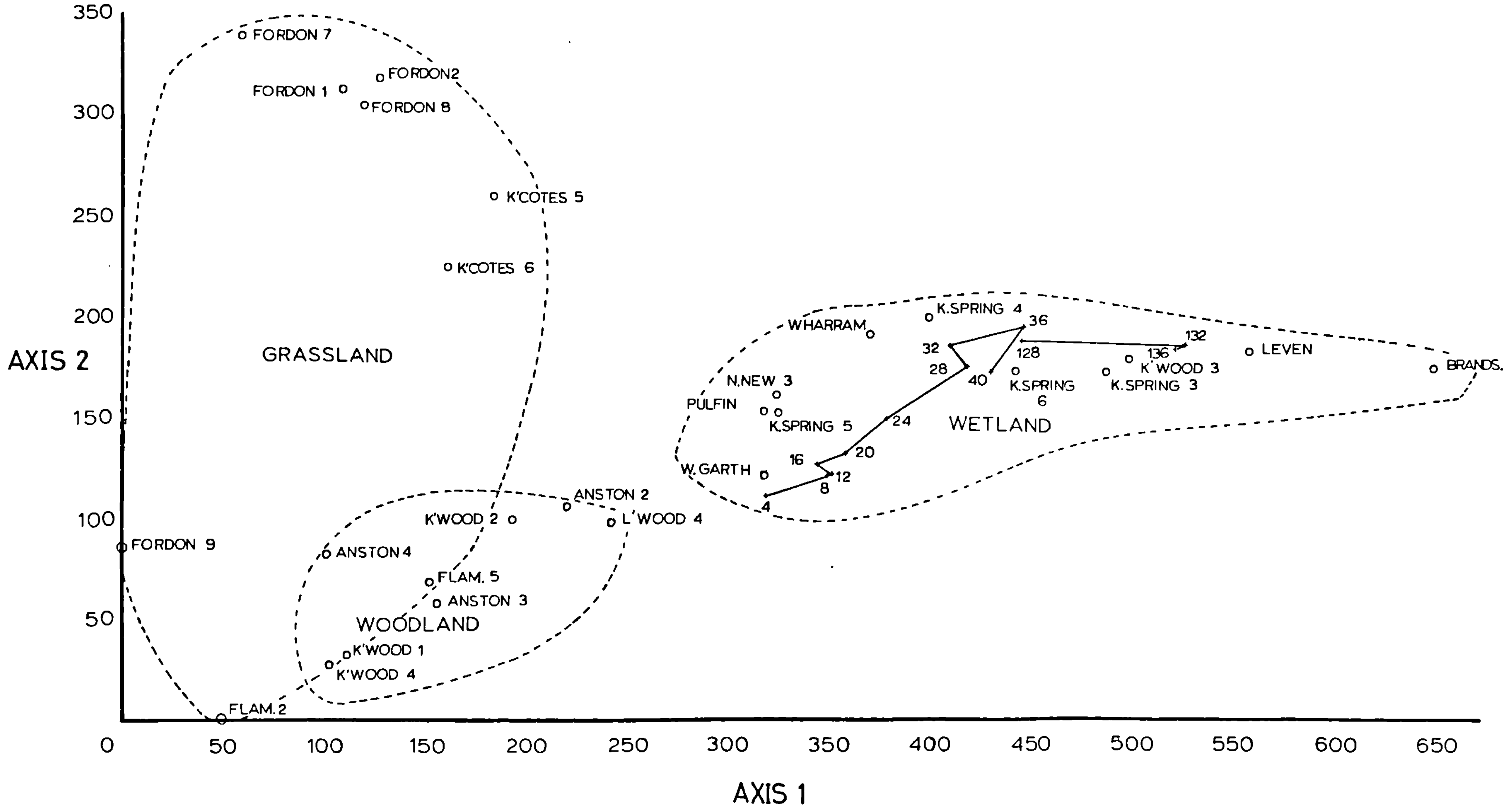


FIG. 7.21 RESULTS FROM THE DECORANA ANALYSIS OF MODERN AND FOSSIL MOLLUSC DATA. BROKEN LINES MARK POLZON. GROUPINGS OF THE MODERN ANALOGUE SITES. ALL FOSSIL DATA DRAWN FROM WILLOW GARTH.

greatest ecological distance between samples was between 24 and 28 cm. The entire fossil mollusc record lies within the modern wetland assemblage zone although for the most part there are no close modern analogues, the best being the modern faunas of Willow Garth for the more recent assemblages and those of Kingswood 3, Kiplingcotes Spring 3 and Leven Canal for the earlier assemblages.

7.11 SIZE VARIATION IN GRAMINEAE POLLEN

The modern Gramineae pollen size data produced a broadly similar histogram for all the sites. In general there was a modal peak from 24 to 27 µm which frequently accounted for as much as 90% of the pollen in a sample. The size distributions tended to be strongly positively skewed with a long, steadily decreasing, tail of representation in the higher size classes. One exception to this was the bimodal peak at Willow Garth where over 20% of the grass pollen was more than 44 µm, with the largest in the 48 - 49 µm category. This could have been partly due to the influx of cereal pollen from the surrounding fields. However, some of these grains had a small annulus (<8 µm) and this would suggest that the pollen was of wild grasses such as Glyceria spp. (Andersen, 1978).

The lack of variation in these data meant that it was not possible to separate habitat types on the basis of their Gramineae size data. The reason for this may lie in the regional pollen rain being so rich in Gramineae pollen. The effect of forest clearance and the planting of grasses for agricultural and amenity purposes has been to create a Gramineae-rich regional pollen component. The 'background count' is so rich in the Gramineae of rough grassland and Lolium spp. that it masks the nuances of the local Gramineae production. Some evidence for this comes in the general over-representation of Gramineae in the modern analogue sites, particularly of the woodland sites, and the lack of correlation between the contacts recorded in the vegetation analysis and the pollen representation in the quadrats.

As there was no pattern amongst the modern analogues there was no point in combining this matrix with that of the fossil Gramineae sizes.

7.11.1 Comparison of Gramineae with Pollen and Propagule Ordinations

From the work of previous authors investigating pollen sources (Tauber, 1965; Janssen, 1984) and those investigating the dispersal of propagules (Ryvarden, 1971a,b; GreatRex, 1983) it may be assumed that changes in pollen will generally reflect a regional trend whereas propagules will reflect local changes in the vegetation.

The use of DECORANA to test whether the pollen was derived from the local, or regional, source is a separate test from that of a constrained classification analysis e.g. POLZON. The DECORANA analysis takes into account the ecological distances between all the samples, and so can give an indication of the direction and strength of the change. To the computer the Gramineae pollen size data is as ecologically meaningful as pollen or propagule data, and therefore the direction and distances between the groups defined by this analysis are comparable to those from the other data sets.

If the clustering seen in the Gramineae size data corresponds with the local changes in vegetation then it may be assumed that the majority of Gramineae pollen has been derived from the local aquatic, semi-aquatic and marshland species. Thus the hypothesis to be tested is:

Gramineae pollen is locally derived and changes in the size histograms of Gramineae pollen will coincide with changes in the local vegetation.

The null hypothesis is that no relationship exists between the two data sets.

If Figs. 7.14 and 7.22 are compared it may be seen that the changes shown in the Gramineae data match poorly with those from the propagule data. The first Gramineae sample (136 cm) is clustered with groups from higher in the diagram (72 to 104 cm). The DECORANA analysis of the macrofossil data shows this sample to be part of a quite independent group comprised of the samples between 136 and 128 cm. The macrofossil data suggest two steady progressions, one between 128 and 104 cm which leads towards an environmental extreme and then one away from that extreme, between 104 and 72 cm.

The Gramineae data show a steady progression of points between 132 and 107 cm. There then follows a period of some fluctuation, but there continues to be a general progression in the same direction until 71 cm. Thereafter, the direction

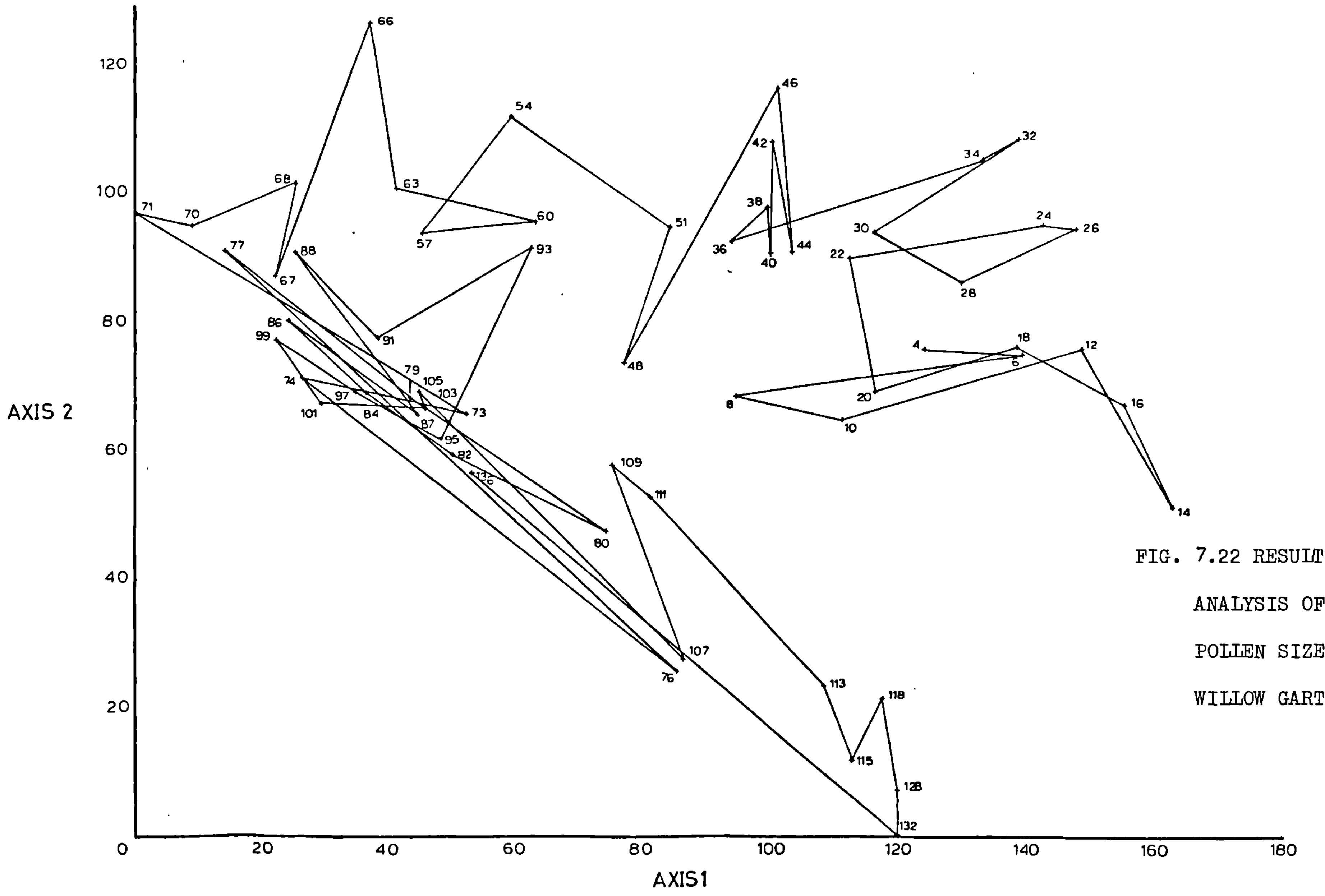


FIG. 7.22 RESULTS OF THE DECORANA ANALYSIS OF FOSSIL GRAMINEAE POLLEN SIZE DATA FROM WILLOW GARTH

reverses until 46 cm where there is a cluster of points. A final loose cluster is made up by the samples between 34 and 0 cm. The macrofossil record shows a tight cluster of points between 72 and 32 cm and then a pronounced change and considerable ecological separation of the final group from 0 to 16 cm. The POLZON analysis showed the timing of the environmental changes were different. The DECORANA analysis shows that the direction of change, and the degree of similarity, between the adjacent samples is quite different in the fossil Gramineae data and the macrofossils. The hypothesis has not been proven and so the null hypothesis (i.e. that there is no significant relationship between the two data sets) is accepted.

A new hypothesis can be tested:

the Gramineae pollen is extra-locally or regionally derived and so the changes in the Gramineae size pollen diagram will coincide with the changes in the fossil pollen analysis.

The null hypothesis, as before, is that there is no relationship between the two data sets.

If Figs. 7.13 and 7.22 are compared, it is immediately apparent that the overall pattern of these two diagrams is very similar. The first point in the pollen data set (Fig. 7.13), 136 cm, is positioned closer to the forest sites of 107 to 68 cm than to the stratigraphically adjacent sample of 132 cm. The environmental trend from 132 to 107 cm and the fluctuations between 107 and 71 cm shown in the Gramineae data are replicated in the pollen analysis. This similarity continues throughout the data sets and it is therefore possible to state that the degree and direction of change between samples is similar in both data sets. This would suggest that the Gramineae pollen is derived from the broad vegetation assemblage represented by the pollen data, that is, from an extra-local or regional source. The relatively small effect of local vegetation change was illustrated by the lack of similarity with the seed assemblage.

The data relating to fossil insects are insufficient to present a zonation based on them and are best presented in a generalised figure (Fig. 7.23). Specific taxa of note will be referred to during the discussion of results (chapter 8). Appendix 3 lists the insect taxa recorded from Willow Garth.

The record of fossil bryophytes is presented in Fig. 7.24.

7.12 SUMMARY OF RESULTS

Eight pollen zones, 11 plant propagule zones and four mollusc zones were noted and described. The suspected depositional hiatus or standstill level at 67 cm was reflected by marked changes in the pollen, Gramineae pollen size and propagule data. Some difference in the timing of vegetational events on a local and a regional level was evident, e.g. in the contraction of <u>Betula</u> representation.

Ordination analyses were carried out on the various fossil data. It was demonstrated that the ordination results based on the fossil Gramineae pollen size samples corresponded more closely with those of the overall pollen samples ordination than those of the ordination of plant propagule samples.

The ecological significance of these results is discussed in the following chapter.

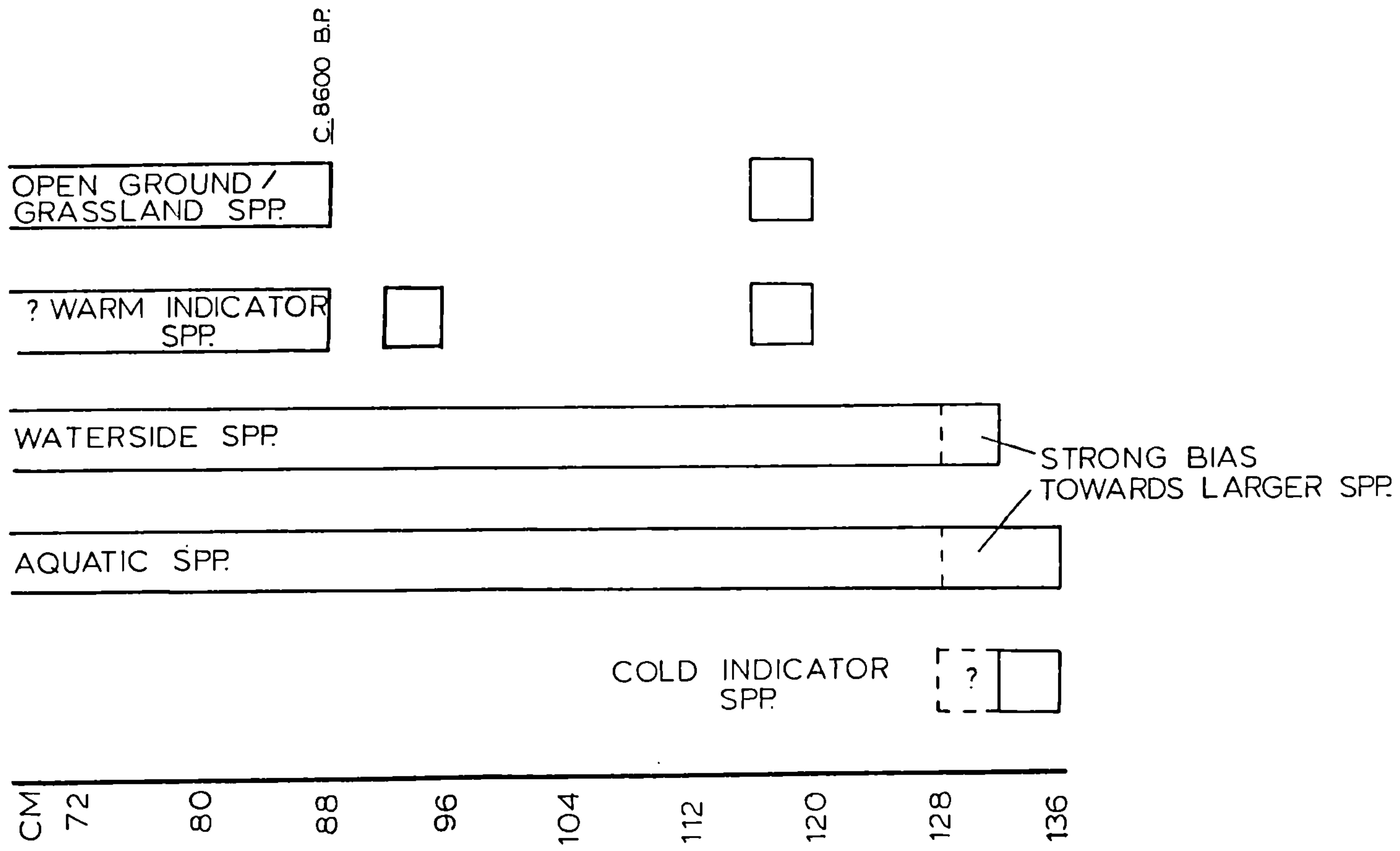


FIG. 7.23 : FOSSIL COLEOPTERAN ASSEMBLAGE DIAGRAM FROM WILLOW GARTH.

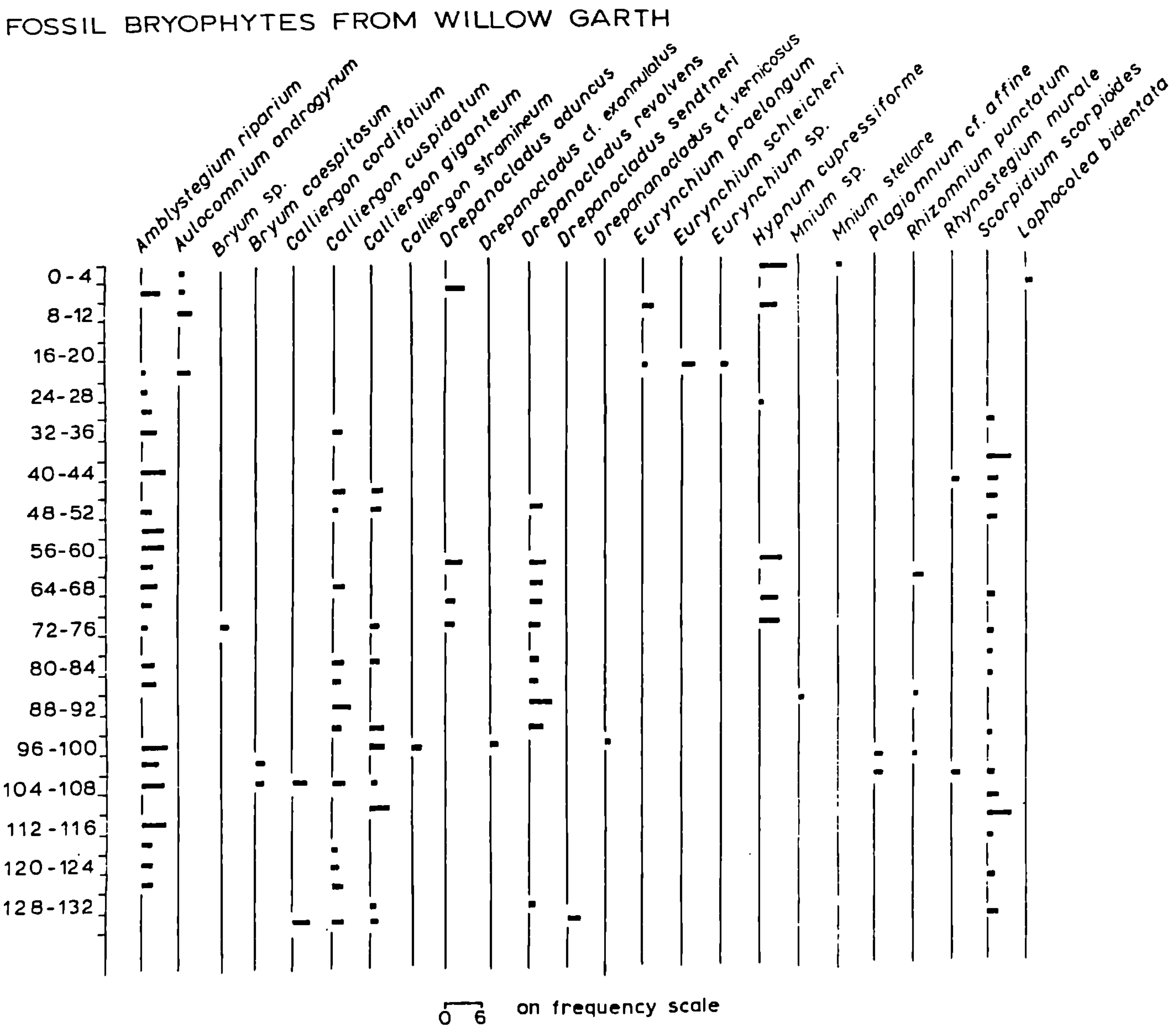


FIG. 7.24 FOSSIL BRYOPHYTES FROM WILLOW GARTH.

CHAPTER 8: PALAEOECOLOGICAL INTERPRETATION

8.1 THE LATE-GLACIAL AND EARLY POST-GLACIAL AT WILLOW GARTH

8.1.1 Biozone WGP-1 (136 - 132 cm)

Sediment

The sediment forming this and the following biozone was a relatively well sorted lens of sandy material with a considerable clay fraction and, rarely, flint fragments. This was part of the gravelly sand deposit described in section 2.2.2. The degree of sorting suggests that the deposit was probably laid down in a low energy fluvial environment.

Biozone WGP-1

Vegetation

The occurrence of Betula nana, Empetrum and Juniperus pollen suggests the presence of shrub tundra. Pollen from tree birch was present at c. 20% of the total dry land pollen. Tree birch can often be stunted under tundra conditions and frequently do not grow above 1 m in height and so could be considered as part of a shrub community. Salix and Pinus pollen were also present, although it is possible that the Pinus pollen had been derived from long distance dispersal. Pinus pollen has been recorded as being the dominant pollen type of modern tundra assemblages even though the closest Pinus was growing over 300 km distant (Ritchie, 1977). Salix although only representing 15% of the total dry land pollen is an under-represented species (Andersen, 1973). When the R-rel values were applied to this species the canopy cover that this represented was indicated to be *c.* 83%.

The macrofossil assemblage contained the bud scales of *Salix* and *Populus* and the fruits of *Salix* and *Betula* (undiff.). This might suggest that the *Betula* and the *Salix* were growing in the sheltered valley bottom whereas the shrub taxa were more distant, growing on the exposed valley sides and tops. The presence of a grain of *Alnus* pollen could be the result of contamination, but other researchers have found *Alnus* in the sediments of zones I, II and III (Beckett, 1975; Scaife, 1980). Grains of *Corylus* pollen found in this sample may have blown in from some distance, or they may represent the local survival of *Corylus* in the sheltered conditions of the valley bottom.

The sizes of the Gramineae pollen of this biozone were generally smaller than in the succeeding layers and were grouped by the TWINSPAN analysis with the samples from the *Betula* dominated spectra of biozone WGP-4.

The submerged aquatic plants *Myriophyllum spicatum*, *Myriophyllum alterniflorum* and *Callitriche* were all represented in the pollen rain. The suggestion of open water conditions is reinforced by the presence of *Helophorus* sp., a beetle which Morgan (1973) notes for its ability to colonise temporary pools. The occurrence of *M. spicatum* and *M. alterniflorum* together would appear to be somewhat unusual as Haslam *et al.* (1975) suggest that they have different habitat requirements. *M. alterniflorum* is said to favour oligotrophic conditions, usually with an acid substrate, whilst *M. spicatum* is suggested to favour eutrophic base rich environments (Haslam *et al.*, 1975). The pollen record of Hockham Mere also revealed the co-existence of these two species at 12,600 ±85 B.P. (Q-2203) (Bennett, 1983). Further evidence of standing pools of water came from the presence of an achene of Ranunculus sec Batrachium and fruits of Potamogeton polygonifolius agg. which were found in this sample. The molluscs of this biozone were Pisidium nitidum, Anisus cf. leucostoma, Succinidae and Cochlicopa lubrica. The first two of these indicate the presence of pools of open water, whilst the two latter taxa indicate fen conditions.

Fen conditions were indicated by the presence of Carex nutlets and the fruits of Menyanthes trifoliata, which is the foodplant of the weevil Notaris aethiops, also found in this sample. In the pollen record Cyperaceae pollen were abundant as were the spores of Equisetum. The presence of a tall fen flora was suggested by the occurrence of pollen of Typha latifolia, Gentiana pneumonanthe, Angelica, Cirsium and Epilobium. A degree of natural disturbance is also indicated by the presence of pollen of Chenopodiaceae and Stellaria media. These plants may have been colonising soil slippages, river gravels, or blown sands. The soils may have been immature or thin, with exposed rocks as these would be the normal substrate for Saxifraga aizoides.

A rich grassland flora is represented in the pollen rain. This was composed of low-growing herbs, ferns and clubmosses, e.g. Rumex acetosa (comp.), Dryas, Liguliflorae, Potentilla, Armeria, Plantago coronopus, Saxifraga oppositifolia, Artemisia, Galium, Botrychium lunaria, Athyrium alpestre (sim.) and Selaginella selaginoides. These could have formed a rich sub-alpine grassland growing between the arctic-alpine shrubs. This is a vegetation type broadly similar to that described from many late-glacial sites (Bartley, 1962; Simpkins, 1974; Beckett, 1975; Bennett, 1983).

The mosses of this level were all species of wide climatic tolerance which live in fens and the margins of fen-pools.

A landscape suggested by these data is a tall fen community containing a pool, or pools, rich in submerged aquatic and emergent plants. The margins of the fen may have carried a mixed birch and willow woodland, which, away from the fen, gave way to a relatively open grassland environment in which arboreal taxa were sparse. An approximate modern analogue may be seen in the transition between sub-alpine grasslands with tall herbs and *Betula* woodlands with tall herb species as described from the Isle of Skye (Birks, 1973).

Biozone WGP-1

Climate

The mosses and molluscs of this zone all have distributions extending from northern Europe into the Arctic-Circle; little can be deduced from these sources of data. Equally uninformative are the plant propagules which are all from plants of a wide climatic tolerance. The 15 *Salix* bud scales found in this level included two which were very small and could have come from dwarf *Salix* species. As the bud size is dependent on the maturity of the twig these could equally well have come from tree *Salix*. There were abundant leaves in this sample which have been tentatively identified as those of Salix repens. This species has a modern Scandinavian distribution concentrated in the south, with only a patchy occurrence north of 60°N. The insect record includes Tachinus sp. and Acidota sp.; both genera contain species which regularly occur in cold assemblages. The only stenothermic insect which could be definitely identified was the weevil Notaris aethiops, a species which inhabits boreal forests (Fig. 7.23). Morgan (1973) recorded this species from Four Ashes, W.Midlands, in an assemblage which she attributed to having come from above the tree-line during the Devensian period. Coope and Brophy (1972) recorded N. aethiops as being restricted to their local zone GLIII at Glanllynnau, N. Wales. A radiocarbon date of 11300 ± 300 B.P. (Gak-1602) was obtained for the base of GLIII, which it is suggested places this zone within the Windermere Interstadial period (Coope and Brophy, 1972). Another interesting record for this weevil is from the Dimlington silts where it was recorded as part of the Boreo-Montane Devensian fauna dated to c. 18200 B.P. (Penny et al., 1969). In this instance it was accompanied, as at Glanllynau, Four Ashes and Willow Garth, by Bembidion spp.. This would seem to have been a widespread wetland fauna during the cold phases of the Late-Devensian period.

The present distribution of Notaris aethiops extends as far south as northern England where it is a rarity restricted to high mountain peaks. Northern Siberia and the northernmost portion of Europe are the only areas where this species is common (Coope and Brophy, 1972). Coope and Brophy suggested that the fauna of GLIII was one characteristic of boreo-alpine conditions of cold winters and mild summers with an average July temperature of c. 14°C.

Such a temperature agrees well with the suggested average summer temperatures of the Windermere Interstadial which Coope (1970, 1977)) gave as declining from 16 - 11°C .

The pollen record contained a wide diversity of herbaceous plants usually associated with tundra or arctic-alpine conditions, e.g. Dryas, Armeria, Saxifraga oppositifolia, Saxifraga aizoides, Betula nana and Empetrum. The present ranges of these plants were shown to be climatically limited by the maximum July isotherm (Connolly and Dahl, 1970) (Table 8.1).

	southern July isotherm limit °C	Scandinavian range southern limit °N
Dryas octopetala	23	59 Sweden
Betula nana	22	58 Sweden
Saxifraga aizoides	24	N/A
S. oppositifolia	23	N/A
Athyrium alpestre	22	N/A

Table 8.1 Data from Connolly and Dahl (1970) regarding the modern climatic and geographic range of selected taxa.

These data would set a southern limit of 59°N. The presence of Corylus avellana and the possible presence of Salix repens indicates that this was not an extreme arctic climate. Hafsten (1956) suggested that C. avellana would not grow unless the mean July to September temperature was in excess of 10.5°C, with mean spring temperatures in excess of 2°C. The

Scandinavian distribution extends to 63°N in Sweden, which coincides with the northernmost limit of the oceanic climatic regime. With *Dryas octopetala* limited to a distribution north of 59°N and *C. avellana* to one south of 63°N, it is reasonable to suppose that the climate of biozone WGP-1 was similar to that which is bounded by those latitudes. This area now has a mean July temperature of *c.* 15°C which does not conflict with the temperature suggested by the insect data.

A further indicator of an oceanic regime is *Empetrum nigrum* (Brown, 1971). However, there has also been the suggestion that the distribution of *E. nigrum* is closely related to podsolisation (Berglund and Malmer, 1971); of course these conditions are not mutually exclusive.

Bell (1969) and Beckett (1975, 1981) suggested that the presence of species generally associated with coastal vegetation associations, e.g. *Armeria*, is indicative of dry conditions. Given that there was an element of drought stress at some time of the year and that temperatures were mild it would suggest that there was less rainfall than at present.

Biozone WGP-1

Relative dating

Radiocarbon dating of the sediment of WGP-1 was not attempted due to the nature of the substrate. From the ecological evidence it is suggested that this biozone corresponds with the Windermere Interstadial, pollen zone II.

8.1.2 Biozone WGP-2 (132 - 129 cm)

Sediment

The sediment appeared indistinguishable from that of the previous biozone.

Biozone WGP-2

Vegetation

A decrease in the *Betula* (undiff.) from 20% to <1% and the disappearance of *Betula nana* and *Salix* pollen indicated increasing openness which may be interpreted as being caused by decreasing temperatures. *Pinus* pollen represented 28% of the total dry land pollen, but as suggested for the last biozone this may represent long distance dispersal. The fruits of *Betula* were found although they represented only 20% of the propagules compared with 39% in WGP-1. Whole *Salix* buds were also found, most of which were very small and may have come from dwarf *Salix* (e.g. *S. herbacea* or *S. repens*). *Salix* was absent from the pollen record in this level. The modern analogue study indicated that local clumps of *Salix* may not feature in a pollen diagram. Thus the buds may have come from willows restricted to the margins of the pool, forming a copse too small to be represented in the pollen rain.

A herb rich grassland prevailed. It contained many arctic-alpine species such as *Lycopodium alpinum* and *Gentiana verna*, in addition to those listed from the last biozone. Evidence of the local occurrence of this flora was also provided by the macrofossil record; fruits of *Lychnis alpina* and *Saxifraga* were found in this level.

Another macrofossil of note was the timber of *Alnus*. This and the two successive levels contained considerable quantities of stem wood of *Alnus*. Identification to species was not possible. This find is discussed more fully in section 8.2.

The fen flora represented by the fruits and pollen appears to have been very similar to that described from the previous biozone, although *Myriophyllum alterniflorum* was missing from this and the two successive biozones. This may be an indication of an increase in the eutrophic status of the pool.

Amongst the 30 mollusc testa recorded from this level, there were 9 species represented, 5 of which were of the genus *Pisidium*. *P. casertanum* will inhabit almost any waters whilst *P. nitidum* and *P. milium* favour well oxygenated, clean water. *P. lilljeborgi* is usually associated with soft water, but does occur at Malham Tarn and Lake Gormire (T. O'Connor *in litt.*). This is a species of upland tarns with gritty, not muddy bottoms (Janus, 1982). Although it is possible that the valve of *P. lilljeborgi* was introduced by a passing bird, its habitat requirements may have been met by the clayey, sandy bottom of a tundra pool: conditions consistent with the sediments in which it was found. The fifth species, *P. pseudosphaerium*, is a species with a disjunct distribution. In its present distribution it is confined to marsh drains in Somerset and Sussex and a marl-pit in Cheshire; the ecological reason for such a distribution is not known (Janus, 1982).

The other molluscan species included *Gyraulus acronicus*, a species which is now restricted to the Thames Basin where it inhabits quiet backwaters rich in algae and aquatic plants. The drainage of wetlands has resulted in a drastic reduction in many hygrophilous taxa. Species exhibiting a local distribution such as that of *G. acronicus* are more likely to be the victims of habitat destruction than climatic change.

There were abundant aquatic flowering plants during biozone WGP-2 and there also appears to have been an abundance of *Chara*. The finest sieve fraction (0.2 mm) of the macrofossil analysis was so full of *Chara* oospores that no attempt was made to count them precisely. The circumstances under which such a flush of oospores might occur could indicate highly favourable conditions in which there were lush growths of the alga, or it could have been unfavourable conditions forcing all the plants to produce propagules.

Whilst the bryophyte data yield no more information than in the previous biozone, the insect data add to the image of a rich aquatic habitat. *Octhebius* were present, these aquatic beetles favour weedy, still or sluggish environments. *Rantus* were also present and by contrast they need weed-free open water. *Geodromicus* generally inhabit a poolside environment, frequenting the semi aquatic mosses. Such a habitat would have been afforded by the *Calliergon giganteum* and *Drepanocladus* spp. identified from this level. The presence of *Daphnia* epiphises also indicates an open water environment with abundant weed.

The overall environment which is indicated was similar to that suggested by Kerney et al. (1964) for the latter part of zone II in the south east of the country, a tundra environment in which tree birches, willows and alder survived in sheltered locations. There was also a rich herb grassland of arctic-alpine taxa with scattered shrubs, and in the valley bottom a rich fen and pool environment. Some of the pools may have been choked by algae and aquatic weeds whilst some, possibly due to greater depth may have been relatively weed free.

Biozone WGP-2 (132 - 129 cm)

Climate

The vegetation was characteristic of tundra and contained many of the arctic-alpine species associated with the previous biozone. In addition to these, there was Lycopodium alpinum which is limited by the 24°C summer maximum isotherm (Connolly and Dahl, 1970). No datum is available for Lychnis alpina, although it has a similar British range to species such as Betula nana and Dryas octopetala (Perring and Walters, 1962). This suggests that the 23 to 24°C summer maximum isotherm might limit the distribution of L. alpina.

The disappearance of Corylus avellana from these samples might be taken as evidence that the thermophilous element of the flora is missing, perhaps suggesting that a climatic deterioration has taken place between this and the previous biozone.

The beetle fauna provided no indication of the prevailing climate as the taxa were only identifiable to a generic level, and all had a wide range of climatic tolerance. It will be noted however that the members of these genera were present in cold stage deposits at Glanllynnau (Coope and Brophy, 1972). The body size of the fauna is biased towards the larger species. Whilst this may be an artefact of preservation, the specimens appear to be well preserved and it may be that the climatic deterioration experienced at this time favoured larger bodied insects.

Biozone WGP-2

Relative dating

It is suggested that this biozone represents the early stages of the Loch Lomond Readvance, or zone III (Godwin 1940).

8.1.3 Biozone WGP-3 (128 - 107 cm), (c. 9500+ - 9300 B.P.)

Sediment

Moss peats with some timber fragments made up the bulk of this deposit. The state of preservation of the mosses was good and many fragments were identifiable to species. This biozone is divided into two sub-zones on the basis of a radical change in the local flora at 112 cm. Sub-zone i) is from 128 to 113 cm, and sub-zone ii) from 112 to 107 cm.

Biozone WGP-3: Sub-zone i), (c. 9500+ - 9400 B.P.)

Vegetation

The species composition of the bryophytes was no different from that of the previous biozones. An explanation for the change to an environment where peat accumulated might lie in an increased input of water to the site allowing permanent waterlogging. This would have prevented the oxidation of the accumulating plant material.

The inititation of peat accumulation may indicate a different source for the water supplying the deposit and a change in the depositional environment. This may have been the start of a spring-fed deposit, or possibly the start of seasonal flooding by the Gypsey Race.

Throughout this sub-zone there was an abundance of arctic-alpine species represented in the pollen and propagule records, e.g. Betula nana, Arctostaphylos, and Empetrum nigrum. Leaves, male catkin fragments and female catkin scales of Betula nana were recorded amongst the macrofossils. Salix bud scales were recorded from most samples and one of Populus was recorded from 120 - 124 cm.

The local dominance of tree birch reached a peak at 116 - 120 cm with 78% of the total propagule sum. This representation was not matched in the fossil pollen record where Betula attained only 2% of the dry land pollen total. The presence of bud scales and catkin scales indicates the growth of a local stand of Betula, which, as indicated by the low pollen yield, may have consisted of only a few trees.

The herbaceous flora was well represented with Gramineae, Cyperaceae and *Equisetum* as the commonest taxa. The arctic-alpine element in this flora was still present and was further diversified with the recording of *Polygonum viviparum* comp., *Campanula* and *Helianthemum*. The palynological separation of *Helianthemum* species is somewhat uncertain and so it is best to leave this identification at generic level. However, it should be noted that in this assemblage *H. canum* might be expected. The assemblage is clearly one of cold, open conditions.

The tall herb community of the fen was well represented in the pollen diagram. An unusual member of this community was revealed in the macrofossil record: two fruits of *Sonchus palustris* were found at 120 to 124 cms. This species, which is now a rarity in the marshes of south-east England, may not be an indicator of a warm climate, but rather that the present distribution results from habitat loss.

Similarly, the dung beetle *Aphodius* (*Heptaulacus*) which was present from two samples in this sub-zone, may also have been the victim of habitat loss, accounting for its modern southern British distribution (H.Kenward pers. comm.). *Aphodius* species will, if really short of food, live on rotting vegetation, but generally they are regarded as indicating the presence of herbivorous mammals. The other insects are a mixture of aquatic and marshland species which enhance the image of the local environment. Whirligig beetles (*Gyrinus* sp.) are predatory beetles generally associated with still or sluggish water with abundant weeds. *Hydrobius fuscipes* is characteristic of stagnant pools, and *Gerris* the pond-skater is another species found in still water. *Donacia* was present, the larvae of which feed on the emergent stems of aquatic plants. The samples were rich in aquatic beetles and their predators such as *Dytiscus*, and the shells of *Caddis* larvae indicate the presence of this frequently carnivorous larva.

No dry land insect taxa were recorded in this assemblage, suggesting that the fen was of considerable proportions. The known aquatic fauna would have utilised the following foodplants: *Groenlandia densa*, *Myriophyllum* sp., *Potamogeton* spp., *Typha* spp. and *Ranunculus* sec *Batrachium* and in the uppermost sample of this group *Cladium mariscus*.

With the onset of peat formation the mollusc record is lost and there are only scattered records of species such as *Pisidium nitidum*, *Aegopinella nitidula*, *Cochlicopa lubrica* and *Succinea putris*. These add little to the image of the environment at that time. The peats were formed of *Calliergon* spp., *Amblystegium riparium*, *Drepanocladus* spp., and *Scorpidium scorpioides*.

Overall it would appear that there was a local *Betula* wood which was growing in the sheltered valley bottom amidst a tundra association of pools and hummocks. Arctic-alpine scrub and grassland grew in the drier areas, and may have dominated the tops of the Wolds. The numbers of *Arctostaphylos* and *Empetrum nigrum* fruits present in the macrofossil samples suggest the local presence of these plants, perhaps growing on hummocks in the fen.

In modern tundra regions the density of wildlife is seasonally variable, but during the summer the grazing impact of geese and deer can be immense. Grazing and trampling are particularly severe along migratory routes or around favoured water-holes. It is possible that the presence of dung beetles indicate that grazing herds had reached the Wolds at this time. Grazing animals could have acted as vectors of dispersal for some of the plant propagules found in the deposit. This could offer an alternative explanation for the presence of fruits of dry land taxa such as the arctic-alpine shrubs amidst what would appear to have been an extensive sub-arctic fen.

Biozone WGP-3: sub-zone i)

Climate

Climatic conditions similar to those of the previous biozone are indicated. Arctostaphylos, represented in this sub-zone, is limited by the 24°C maximum July isotherm (Connolly and Dahl, 1970). The continued absence of Corylus avellana from the pollen spectrum suggests that sub-arctic conditions continued into the early stages of this biozone. No stenothermic insect taxa were recorded, possibly due to the difficulty of identifying the elytral fragments to species level. Genera present in these levels such as Bembidion and Colymbetes, and the Hydrophylline group, are often abundant in 'cold' faunas, but they can also be found in temperate assemblages.

One record which does stand out is that of 10 fruits of Cladium mariscus at 116 to 112 cm. Von Post (1925) suggested that C. mariscus is intolerant of continental conditions and this was confirmed by the experimental work of Conway (1938) who demonstrated that C. mariscus is frost-sensitive. This would imply that a marked climatic amelioration was taking place at the end of this sub-zone. The modern northern limit of C. mariscus in Scandinavia is 60°N which would suggest conditions at least as oceanic as those of biozone WGP-1.

Biozone WGP-3: sub-zone i)

Relative dating

This sub-zone would appear to cover the middle and late Loch Lomond Readvance with the beginning of the change to the Pre-Boreal period represented in the uppermost sample. A radiocarbon date of 9460 ±80 B.P. was obtained from the peat at 115 cm - 118 cm depth. A date which is surprisingly late, suggesting that the lowest carbon date may be too young.

Biozone WGP-3: sub-zone ii) (112 - 107 cm), (9400 - 9300 B.P.)

Vegetation

Pinus and Betula (undiff.) provided the arboreal pollen input into a relatively open landscape. Whether Pinus was growing locally is still uncertain, but Betula pollen (10%) was more abundant than in the previous sub-zone. This increase was not paralleled in the macrofossil record where Betula fruits dropped from 70% to 30% of the total count (770 to 162 fruits per litre). Betula catkin scales also disappeared from the record during this sub-zone. This would imply that the local occurrence of Betula, as seen through the macrofossils, was reduced, but that the overall abundance of Betula, as indicated by the increasing pollen count, was greater. An increase in the concentration of *Carex* nutlets and fruits of *Valeriana*, *Menyanthes trifoliata* and *Mentha* suggest that the fen environment was expanding.

The arctic-alpine species all disappeared during this sub-zone, leaving a herb rich grassland containing such taxa as *Campanula*, *Helianthemum* and *Achillea* agg.. These were species of short grassland communities rather than a tall fen association. The grassland taxa may have been growing in the drier areas in an open association with some *Betula pubescens* and *Empetrum nigrum*. Pollen of *Calluna* might be indicative of long distance transport from the North York Moors, or *Calluna* may have become established on the till sheets, or possibly as a calcareous heath formation on the immature chalkland soils of the Wolds (Grubb *et al*., 1968). However, the most likely explanation is that *Calluna* was growing on the sandy hummocks in the Great Wold Valley.

The fen vegetation appears to have been a tall herb community containing: *Filipendula*, *Epilobium*, *Polemonium caeruleum*, Cyperaceae, *Lychnis flos-cuculi*, *Valeriana*, *Succisa pratensis* and *Equisetum*. There were also the emergent species and sub-aquatics recorded in the previous sub-zone.

The grassland species diversity appeared to decrease in both the fossil pollen and the macrofossil record during this period. At 112 cm two large Gramineae pollen grains were recorded, one of 48 µm and the other of 50 µm, but the small size of the annulus (7 µm) indicated that these were wild grass types. The wild grasses most likely to attain this size are *Elymus arenarius* or *Agropyron pungens* (Beug, 1961). Both of these are halophytic and would not normally be associated with inland lowland environments. Their ocurrence in the Great Wold Valley is less surprising in view of the presence of other coastal and montane species, e.g. *Armeria maritima*. Similar large Gramineae have been recorded from the late-glacial of the Isle of Wight, and were also interpreted as probably being derived from halophytic grasses (Dr R.Scaife pers. comm.).

The decrease in species diversity might be due to the loss of the arctic-alpine flora (Fig. 8.1), probably due to the climatic amelioration, and a lag before the influx of temperate species.

During this sub-zone the bryophyte flora diversified with *Plagiomnium* cf. *affine*, *Bryum caespitosum* and *Rynchostegium murale* appearing for the first time. *Calliergon cordifolium* reappeared after an absence since biozone WGP-1. None of these mosses are indicative of specific climatic traits, although all favour a shaded or moist environment.

The insect fauna is a rich aquatic assemblage similar to that described in the previous biozone. Again no terrestrial species were found in the assemblage.

The overall habitat would appear to be one of ameliorating climatic conditions favouring woodland development, although there is still a strong grassland element in the landscape. In the valley bottom a spreading and diversifying fen flora may have forced birch to retreat off the centre of the fen, possibly due to a rising water table.

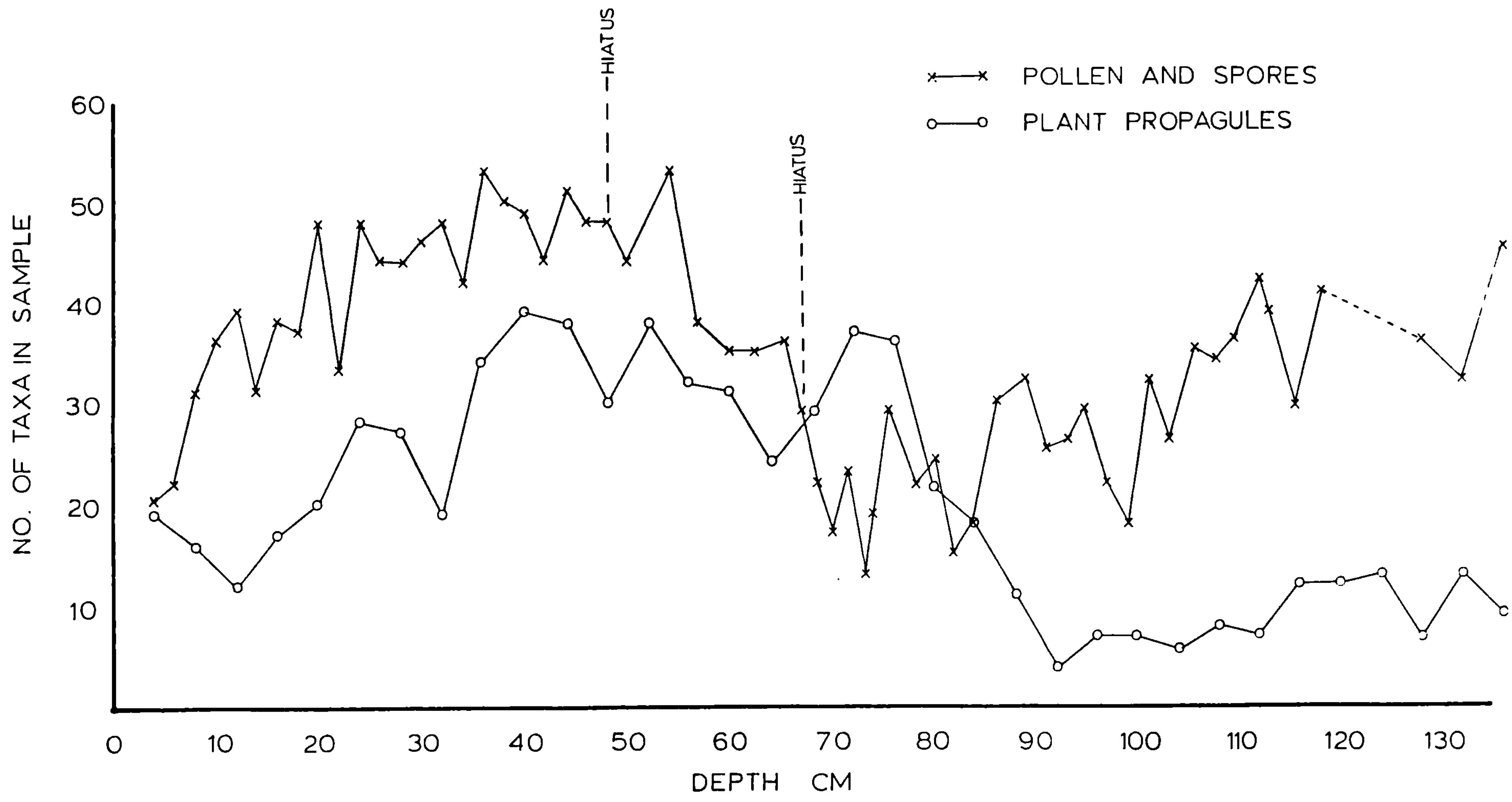


FIG. 8.1 FOSSIL POLLEN AND PROPAGULE DIVERSITY IN SAMPLES FROM WILLOW GARTH

Biozone WGP-3: sub-zone ii)

Climate

In this sub-zone the climatic amelioration suggested by the presence of Cladium mariscus at 112 to 116 cm is now confirmed by the disappearance of the arctic-alpine and halophytic species after 109 cm. Oceanic species, e.g. Empetrum nigrum, increased and Filipendula and Corylus returned to the flora. Some taxa which had been components of the late-glacial grassland were still represented, e.g. Campanula and Helianthemum. However, these may have been different species from those in the previous biozones.

Increased moisture availability is indicated by the increased abundance of fenland taxa and the retreat of the birch as the fen expanded. This may have come about through increased precipitation. Alternatively, the climatic amelioration would have resulted in soil moisture being released earlier in the year. The last macrofossil record of Betula nana was at 116 cm. This species is limited by the 22°C summer isotherm (Connolly and Dahl, 1970), and further warming is apparent from the loss of Arctostaphylos (limited by the 24°C summer isotherm) from the fossil record at 108 cm. This implies a rise of c. 2°C in the summer maxima over a period of c. 300 years, between c. 9600 and 9300 B.P..

8.2 THE PRESENCE OF ALNUS IN LATE-GLACIAL DEPOSITS

Alnus has been recorded from deposits in all the Pleistocene stages since the Pastonian (Godwin, 1975). However, there remains the difficulty of identifying members of the genus to a specific level. The pollen is variable and although Praglowski (1962) suggested how to separate the pollen of *A. glutinosa* from *A. incana* very few palynologists attempt this distinction.

During the post-glacial period many pollen diagrams show a progressive increase in *Alnus* during zone VI and then there is a rapid rise at the beginning of zone VIIa to reach modern levels. In zone VI *Alnus* may well have been a common forest component, not merely restricted to wetland areas (Godwin, 1975; Praglowski and Wenner, 1968).

The possibility that the *Alnus* timber samples from Willow Garth, found between 120 - 132 cm, might have been derived from younger deposits must be considered. There is the possibility that someone once tried to drive an alder stake into the ground and the tip broke off. This timber did not come from a very thick branch and it may therefore be considered as unlikely material to use for fencing. In addition to this it showed no sign of belonging to a single piece, and much less of having been worked. The levels in which it is found show a sharp boundary with those above them and so it is unlikely to be derived from any form of mixing from above. The peats above have been dated to 9460 ± 80 B.P. (SRR-2674) which, in all probability, provides a minimum age for the timber. The deposits in which the timber occurs are suggested to have been formed during the Loch Lomond Readvance implying a date of c. 10000 B.P., or earlier.

There remains the possibility that this is reworked timber from previous interglacial deposits. This possibility can only be disproved satisfactorily by radiocarbon dating of the timber. However, as the timber was found in three separate samples, laid down under changing environmental conditions, it would appear that these fossils were not the product of a single depositional event. In brief, there is no evidence to suggest that this timber should not be accepted as occurring *in situ*.

Three of the pollen diagrams near to Willow Garth showed *Alnus* pollen in samples from the late-glacial onwards: Brandesburton (Clark and Godwin, 1956), Roos and Hornsea (Beckett, 1975). The possibility of long distance transport should not be overlooked. Nevertheless, the pollen occurred at all the sites, and such a consistent representation might argue for a not too distant source.

There do exist other records of *Alnus* peaks during the late -glacial period. One such peak is shown in the Windermere Interstadial in a pollen diagram from the Isle of Wight (Scaife, 1980). The pollen which formed this peak may have been derived from stands of *Alnus* in what is now the English Channel. The scattered stands of *Alnus* which Firbas (1949) suggested as having existed on the North German Plain during the Pre-Boreal period may have extended into the English Channel and the North Sea Basin. In view of this, it is not so surprising to find remains of *Alnus* in eastern England at such an early time.

Pollen was found at the three Holderness sites during zone

III but there is no record of fruits or pollen from this period at Willow Garth. It is possible that Alnus had invaded the east coast of England during the Windermere Interstadial period but failed to survive in some locations throughout the cold of the Loch Lomond Readvance. The timber at Willow Garth could represent moribund trees, killed by the climatic deterioration, which have toppled into the fen. Remains of Alnus are not recorded again at Willow Garth until 92 - 96 cm (c. 8800 B.P.) where there is a fruit, this being the first of a continuous sequence of records of Alnus through to the present day.

Whether the Alnus represented in the late-glacial of Willow Garth was A. glutinosa or A. incana is not apparent from the timber samples as the two are morphologically similar. The present distribution of A. glutinosa extends to 64°N in Sweden (Fitter, 1978). The record of this species as a tree of western Scandinavian mountains existing as an altitudinal belt between the Pine and Birch zones is significant (Praglowski and Wenner, 1968). This is strong evidence that A. glutinosa can occur naturally in non-wetland locations, an important finding in the consideration of past environments. A. glutinosa seedlings are intolerant of late spring frosts, but otherwise the tree is extremely hardy and has a considerable tolerance to the cold (McVean, 1953). The tolerance of Alnus glutinosa led Godwin to comment:

> "It seems probable that it (A. glutinosa) was present in locally favourable situations long before its general extension, and perhaps from the end of the Late Weichselian."
>
> (Godwin, 1975 p.268)

The timber from Willow Garth is the best evidence yet of the presence of Alnus in England during the late-glacial period. That there may have been a local extinction of the tree during zone III suggests some climatic sensitivity; this might be evidence that the species was A. glutinosa rather than the more northerly distributed A. incana.

8.3 THE PRE-BOREAL AND BOREAL FOREST

8.3.1 Biozone WGP-4 (106 - 97 cm), (c. 9300 - 8900 B.P.)

Sediment

Moss peats as described above.

Biozone WGP-4

Vegetation

This zone marks the sudden increase of Betula pollen. It took c. 100 years for Betula pollen to increase from 12.5% to 58% of the total dry land pollen. A similar rate of expansion was noted by Bennett (1983) from Hockam Mere where it took 85 years for the Betula forest to reach its Pre-Boreal equilibrium. It has been suggested that Betula pubescens was the tree which was responsible for the dominance of the Betula forest in the early post-glacial period (Godwin, 1975). This hypothesis is supported by the identification of a well preserved leaf of B. pubescens from the sample at 100 to 96 cm from Willow Garth.

The macrofossil record indicates the local abundance of Betula was relatively constant throughout this biozone and remained largely unchanged from the frequency of the previous biozone. The fluctuations that exist in the Betula fruit record from these levels could be explained by fluctuations in the fen margin. This would suggest that the Betula woodland in the valley bottom was constant but that birch woods were becoming established on the chalk outcrop.

Pinus pollen which had been consistently present at about 28% in the preceding biozone fell to a constant 3% to 5% throughout this zone. The number of grains per gram had not altered, remaining at c. 5000, and this may be the level of long distance input. This suggests that c. 5000 grains g^{-1} should be taken as the 'background count' for Pinus pollen.

Obligate aquatic taxa are absent from the macrofossil record during this period although there was an increase in the fenland component, e.g. Carex disticha and Pedicularis palustris, which may indicate a drying of the fen. The fenland taxa would have been expected to increase in abundance as they invaded the drying pools. The pollen record suggests the presence of a fen meadow community, including Polemonium caeruleum, Sanguisorba officinalis and Orchidaceae. Orchidaceae, despite producing a highly distinctive pollen type, are seldom recorded in British pollen diagrams. The low pollen production, entomophily and poor pollen preservation of this family contribute to their poor representation in fossil samples. However, Orchidaceae were well represented in the pollen assemblage from Willow Garth. In those samples where there was a regular occurrence with up to 3% of the pollen sum it probably indicates that the orchids were growing on, or near, the sampling point and collapsing directly into the fen. The alternative, and not mutually exclusive, explanation is that the orchids were once a much more important component of a calcareous fen flora.

The nearby presence of standing water was suggested by the pollen of Myriophyllum spicatum, Potamogeton and Typha latifolia. Poolside and fen mosses were abundant and amongst these, Calliergon stramineum, Drepanocladus exannulatus and D. vernicosus appeared for the first time. The aquatic fauna appears to have been very similar to that described from the previous biozone.

The continued presence of grassland in the landscape is suggested by the high values of Gramineae (25% to 42% of dry land pollen sum) and the presence of the dry grassland taxa: Helianthemum, Campanula, Plantago media/major and Botrychium lunaria. Whether these existed in a very lightly shaded woodland community, or in open areas within a birch woodland is uncertain. However, it is clear that the woodlands were not sufficiently dense to exclude these light demanding species.

Overall it would seem that the expansion of the Betula pollen heralds the arrival of the Pre-Boreal forest at Willow Garth at c. 9300 B.P.. This is later than at Hockham Mere where the arrival was dated at c. 9600 to 9400 B.P.. Such a discrepancy could be attributable to dating errors or the rate of expansion of Betula on different geologies and at different latitudes. Although Betula became established it failed to dominated the landscape and the chalk grassland persisted.

Biozone WGP-4
Climate

It is probable that Betula had been growing in the valley bottom for several hundred years before this expansion to form the Pre-Boreal forest took place. This might suggest that at around 9300 B.P. there was a sufficient climatic improvement to allow a more rapid expansion of Betula out of the valley bottom and to colonise the exposed slopes of the Wolds, a process which had started in the previous biozone. The first record of the thermophilous species, Sanguisorba officinalis, which has a present distribution south of 62°N in Sweden (Godwin, 1975), may be a further indication of climatic improvement at this time.

The decrease in the aquatic taxa suggests a net drying of the environment. The drying may have been a purely local phenomenon. If this was a regional decrease in water availability it would suggest a regime of increasing temperatures without a compensating increase in precipitation.

Biozone WGP-4
Relative dating

The sudden expansion of the Betula forests marked the Pre-Boreal forest of zone IV. West (1968) suggested a date for this period of 10250 - 9400 B.P., which is slightly earlier than the 9300 - 8900 B.P. suggested for Willow Garth.

8.3.2 Biozone WGP-5 (96 - 68 cm), (c. 8900 - 7980 B.P.)

Sediment

A moss peat as described above made up most of this deposit, but there was a band of timber-rich peat from 76 to 82 cm.

This biozone was subdivided into two sub-zones on the basis of the macrofossil record. Propagule diversity started to increase at 84 cm, but in ecological terms the division at 74 cm suggests a greater environmental change. The sample at 74 cm was shown by the DECORANA analysis, of both the pollen and propagule data, as being a level where a change of ecological direction took place.

Biozone WGP-5: Sub-zone i) (96 - 74 cm), (c. 8900 - 8200 B.P.)

Vegetation

This sub-zone was characterised by the first occurrence of the trees associated with the transition from the Pre-Boreal to the Boreal forests. Betula was still the commonest arboreal pollen type, although in the early part of this biozone, from 96 - 87 cm this dominance was reduced by the presence of Pinus. At 96 cm there would appear to be an increase in Pinus pollen which was reflected in the absolute values as well as in the percentage data. Pinus attained a peak of 30% of the dry land pollen (14500 grains g^{-1}). This may represent the Pinus peak at the beginning of pollen zone V which is common to many British pollen diagrams (Godwin, 1975). In the Great Wold Valley the sandy deposits on the valley sides would offer suitable sites for colonisation by

Pinus.

Quercus pollen began to occur regularly and *Corylus*, *Fraxinus* and *Salix* pollen were also present. Macrofossils of *Alnus* were found from 96 - 92 cm onwards. First, there was a single fruit, and then some timber at 92 - 88 cm.; at 84 - 80 cm there was an entire male catkin and two fruits. The sample from 80 - 76 cm was rich in timber, most of which was identified as *Salix*, but it also contained fragments of *Alnus* and *Quercus*. A *Quercus* leaf and bud scale were also extracted from this sample.

The diversity of fruits increased markedly during this biozone, from 4 types in the sample at 92 - 88 cm to 33 taxa at 76 - 72 cm (Fig. 8.1). Many of these were fenland and submerged aquatic species. The fen had been a sedge swamp at the beginning of the sub-zone with sedge nutlets accounting for 50% of the local propagules. Almost all the remainder were *Betula*. At 88 - 84 cm the fen became wetter, as indicated by the presence of fruits of taxa such as *Potamogeton*, *Sparganium*, *Hydrocotyle vulgaris*, *Ranunculus* sec *Batrachium* and *R. flammula*. The pollen record shows an increase in the tall herb community of the fen, particularly of *Filipendula* which attained values as high as 30% of the total dry land pollen sum at 89 cm. The dominance of the fen flora by such a tall herb as *Filipendula* does not preclude a diverse flora, as can be seen at modern fens such as North Newbald fen. Here smaller, earlier flowering species manage to survive amongst a tall *Filipendula ulmaria* community. A period of wetland expansion is suggested and this argument is supported by the sudden decrease in the representation of *Betula* in the propagule record, from concentrations of 360 fruits per litre at

96 cm to 20 fruits per litre at 84 cm. This probably reflects a retreat of *Betula* before an expanding fen margin. The modern analogue study suggests that for the representation of *Betula* to fall this low would require the nearest source of *Betula* fruits to have been more than 50 m distant. This implies that the fen was over 100 m wide at this time.

The pollen record does not show a contemporaneous drop in the *Betula* pollen influx, which implies that the pollen was derived from a wider source area than that of the fruits. The diagram obtained using R-rel weighting factors suggests that *Betula* was still the dominant forest component. However, the model would appear to have been invalidated because of the distance of the trees from the sample site. This finding would not be apparent from the use of pollen data alone. In the modern analogue studies *Betula* was shown to be an extremely efficiently dispersed pollen type, as indicated by the high intercept position Po obtained in the R-rel calculations. It may therefore be expected that *Betula* would have been even more over-represented in a pollen diagram when the trees were all at a distance in excess of 20 m from the sample site.

Unfortunately, the decrease of *Betula* was not dated for any of the Holderness sites but it appears to have been a rapid decline once the more thermophilous forest taxa had arrived (Beckett, 1975). A similar rapid decline is apparent at Hockham Mere as soon as the *Pinus* and *Corylus* curves start to increase. This pattern was not repeated at Willow Garth where *Betula* was apparently still a dominant forest taxon when *Corylus* and *Pinus* were dominant in most other parts of lowland Britain.

Another unusual feature of the data from this sub-zone is the evidence for unforested dry land areas at a time when other parts of the country were clad in dense forest. Breaks in the woodland cover are suggested by the presence of the pollen of open ground taxa, e.g. Lotus, Bellis, Plantago lanceolata, P. media/major, Centaurea nigra, Polygonum lapathifolium and Chenopodiaceae. This is supported by the high percentages for Gramineae pollen which reached values of 38%. Only in the uppermost levels of this biozone does the Gramineae representation fall below 20%. The size range of the Gramineae pollen within these samples is also important. The TWINSPAN analysis of the Gramineae size data, placed the sample from 93 cm into a different group of levels from those below it. This sample was grouped with levels in which there is clear evidence of woodland disturbance and clearance (56 - 50 cm). This separation was made at the first divisive level, indicating a strong statistical difference in the size distribution of the pollen in this level, from those below it. The neighbouring level at 91 cm was misplaced at the first division of the TWINSPAN analysis, indicating how close that sample was to also being placed in the same group as the sample from 93 cm. Four consecutive levels from 93 - 87 cm contained Gramineae pollen larger than 44 µm in length, with annuli up to 11.5 µm wide. After inspection these grains were considered to be of Avena or Hordeum type (Dr R. Scaife pers. comm.). This is discussed further in section 8.4.

The propagule spectrum from the levels between 88 and 76 cm included disturbed ground taxa, e.g. Chenopodium album, *Atriplex patula* comp., *Stellaria media*, *Aphanes microcarpa*, *Rubus idaeus* and *Ranunculus* sec *Ranunculus*. The presence of *C. album* is particularly striking as this is a species which will not grow in fen, woodland or grassland but needs disturbed ground in order to germinate. The regular occurrence, and the presence of as many as 7 fruits in one sample, suggests that this was not a chance record.

The insect assemblage contained a variety of wetland species, including: Hydrophillines, *Ochthebius* sp., *Hydraena* sp., *Limnebius* sp., *Donacia* sp., *Baris* sp., *Bagous* sp. and *Chaetarthria seminulum*. These represent a range of still water and pool margin habitats, e.g. *C. seminulum* which inhabits mud and moss at the edge of pools (Balfour-Brown, 1958). A striking feature of the insect assemblage in this sub-zone is that after a series of assemblages containing nothing but aquatic and semi-aquatic species there began a succession of samples from 88 to 64 cm in which *Philopertha horticola* occurred in every sample. *P. horticola*, the Garden Chafer, is a grassland species the larvae of which feed on roots, especially those of dry land grasses. This species is a relatively large beetle which is unlikely to occur consistently in a deposit as a member of a background fauna. H.Kenward, who identified the insect remains, commented that:

> ".. the beetle's presence in several samples doubtless is indicative of clearance."
>
> (H.Kenward *in litt.*)

Also present in this sub-zone were *Serrica brunea*, another grassland chafer and *Cantharis rustica*, the Soldier Beetle. *C. rustica* is a terrestrial beetle which lives in organic litter during its larval phases. As an imago it spends much of its time sitting on flowers, notably those of the Umbelliferae, and is a common insect of grassland assemblages (Balfour-Brown, 1958). *Pterostichus diligens* and *Cymus* which also occurred in these levels can be found in a variety of dry land and fen habitats.

The evidence from the palaeoecological record reveals that there was a change taking place in the local and regional environment during this biozone. The temperate forest species were arriving, but the transition to a mixed temperate forest appears highly atypical. The evidence portrayed by Willow Garth is of a spreading and diversifying fen flora, the retreat of birch woodland and the arrival of pine, swiftly followed by the first records of temperate deciduous forest taxa. The expected dominance of this forest did not take place as there were still taxa present indicating areas of open grassland and soil disturbance. The possible explanations for this series of events are dealt with in section 8.4.

Towards the end of this sub-zone there was a marked drop in the species diversity of the pollen spectrum and the presence of *Betula* increased to 68%. This could represent a regrowth of the *Betula* forest, although the open ground indicator *P. horticola* was still present. After this phase, which lasted from 84 - 80 cm there was a renewed diversification of the pollen spectra, with an increase from 15 pollen and spore taxa at 82 cm to 29 taxa at 75.5 cm.

The pattern depicted by the DECORANA analysis is of particular interest. The Betula woodlands appear to be divided into three groups (Fig. 7.17), from 105 - 95 cm, 93 - 86 cm (separated on the grounds of direction of ecological change. See Fig. 7.17) and 84 - 74 cm. The samples at 105 - 95 cm and 93 - 86 cm would appear to be ecologically similar. The earliest of these groups shows a trend towards the negative extreme of the second axis. It has been suggested that this axis represents an edaphic gradient, e.g. decreasing pH. This would be in accord with the evidence of decreasing pH in these sediment samples. This could be interpreted as the establishment of a Betula woodland, for which there is no modern analogue. Between 95 and 97 cm there was a trend leading to denser forest, until at 93 cm this trend is reversed and an ecologically different woodland develops. The newly formed woodland appears to be a close match with one of the modern analogue Betula woodlands taken from the data set of Birks (1973). The analogue woodland was an open birch forest with a high (30%) Gramineae component. From 84 cm there is a progression towards the negative extreme of the first axis, suggesting a denser woodland cover. After a slight movement away from this axis between 77 and 74 cm there begins a trend out of the Betula forest zone. The DECORANA analysis would therefore show two periods of forest disturbance, one from 93 - 86 cm, and another from 77 - 74 cm. Following this last disturbance episode there was a rapid change in the woodland ecology as a temperate deciduous forest began to dominate the Betula forest.

The data obtained in the preliminary survey are in broad agreement with those of the main study. The preliminary core was extracted from a point approximately 2 m from the main core, but the plants forming the extra-local and regional inputs follow a similar pattern (Appendix 1). It can be seen from the preliminary pollen diagram that the hiatus probably occurred at c. 75cm. A radiocarbon date was obtained from the section 96 - 92 cm giving a date of 8160 ±150 B.P. (HAR-5064). In the samples between the base of the peat at 96 cm and the hiatus at 75 cm there was a regular occurrence of Plantago lanceolata and Centaurea nigra. Helianthemum and Sanguisorba minor were also present below the hiatus.

Biozone WGP-5: sub-zone i)

Climate

There were climatic indicator taxa in the insect, propagule and pollen data for these levels. At 96 - 92 cm an elytron of Metopsia retusa, an insect now restricted to a very southern Scandinavian distribution, and the occurrence of Philopertha horticola, which does not extend north of 64°N in Sweden, suggest a climate as warm as or slightly warmer than the present day. This is supported by the occurrence of Cantharis rustica, an insect restricted to a distribution south of 62°N in Norway.

The presence of propaguless of Ajuga reptans, Eupatorium cannabinum and Moehringia trinervia, plants which today have Swedish distributions south of c. 61°N, confirm that this was a temperate climatic period. The most thermophilous of all the climatic indicators is represented by two pollen grains of Teucrium botrys, at 77cm. T. botrys is a calcicolous plant with a modern British distribution limited to a few locations on the southern downs. The southern scarps of the North Downs are the northernmost limit of the European range of this plant. For T. botrys to have occurred in Yorkshire suggests a climate at least 2 - 3°C warmer than present.

Precipitation must also have been substantially increased for the marshland to have expanded in a period of increasing temperatures.

Biozone WGP-5: sub-zone i)

Relative dating

This sub-zone would appear to have covered zone V and early zone VI of the Flandrian. The boundary between the two is generally indicated by the rise of taxa such as Quercus and Ulmus and the decline of Betula and Pinus. That forest disturbance prevented the full development of a traditional zonation does not hide that at c. 96 - 92 cm there was evidence of the climatic amelioration which heralded the start of zone VI. This would indicate a date of c. 8800 B.P. for the start of zone VI at Willow Garth.

Biozone WGP-5: sub-zone ii) (74 - 68 cm), (c. 8200 - 7980 B.P.)

Vegetation

The sedimentation throughout this period resulted in a moss peat in which there is very little woody material. The percentage organic carbon content is consistent at c. 7% to 8%. The moss matrix is dominated by the remains of Calliergon giganteum and

Scorpidium scorpioides indicating a poor fen habitat.

The pollen record shows that there was a decline in species diversity at the beginning of this sub-zone (Fig. 8.1). At 73 cm there were only 13 taxa represented. One species, Betula, accounted for 58% of the dry land pollen total.There then followed a period of increasing pollen and spore diversity until the end of the biozone.

In the macrofossil assemblage the woodland flora was represented by Arenaria and Alnus; Betula was reduced to 2% to 3% of the total propagule count. In the pollen sum after the resurgence of Betula there is a peak of Pinus reaching 43% at 70 cm. Filicales spores increased alongside the Pinus during this period attaining values as high as 60% of the total pollen (108% of the total dry land pollen), at 68 cm. Whilst it may be argued that peaks of Pinus and Filicales are frequently associated with selective preservation the concentration of pollen and spores in these samples ranges between 100,000 grains g^{-1} and 740,000 grains g^{-1} without any corresponding fluctuation in the Pinus and Filicales totals. This may be taken as evidence that these are genuine peaks of local production and are not the products of selective destruction. The DECORANA analysis (Fig. 7.17), from which Pinus and spore taxa were excluded, reveals a rapid migration from Betula forest to the fen woodland complexes represented above the hiatus. The fen element in the pollen record prevents the line, which represents the fossil habitat sequence, from passing through the dry modern analogue woods.

The diversity of macrofossils declined after 72 cm from a peak of 37 propagule taxa to 29 taxa at 68 cm. Both of these represent an extremely diverse flora, but to compare them directly is not profitable as the sample 68 - 64 cm spans the hiatus in the core at 67 cm. The macrofossil data will therefore refer to the sample 68 - 72 cm, as this is the only macrofossil sample to lie entirely within the sub-zone. The evidence for a rich fen community is apparent with species such as *Lythrum salicaria*, *Pedicularis palustris*, *Lychnis flos-cuculi*, *Cladium mariscus*, *Eleocharis* and *Juncus* spp.. There was a highly diverse aquatic flora, with: *Bidens tripartita*, *Sparganium*, *Ranunculus* sec *Batrachium* and *Potamogeton* spp.. The return of *Myriophyllum alterniflorum* may suggest a decrease in the eutrophic status of the pool, or some locally acid pools.

Aphanes arvensis, *Chenopodium album* and *Atriplex* were present, indicating that there was still a degree of soil disturbance. Other grassland indicators included the pollen of *Centaurea nigra*, and the insect *Philopertha horticola*, both of which were present in these samples.

The above evidence suggests a landscape of dense birch regrowth, giving way to a pine woodland, in which open and disturbed ground taxa also survived. The peak of *Filicales* may represent a local growth of ferns on the fen, or these could have been a herb layer in the pine wood.

WGP-5 sub-zone ii)

Climate

The climate would appear to have been the same as at the end of the preceding sub-zone. There were no new climatic indicator species and all but *Metopsia retusa* and *Teucrium botrys* were still present in this zone. This might imply that the peak of the climatic optimum had passed, but equally, it may be that these were relatively rare species which were not likely to be recorded a second time.

WGP-5 sub-zone ii)

Relative dating

The apparent woodland disturbance makes it difficult to place this biozone within the traditional zonation framework. However, the climatic amelioration and the continued presence of *Betula*, *Pinus* and *Corylus*, plus the increasing evidence of *Quercus*, but no *Tilia*, suggests that this might have been mid zone VI which would correspond with the radiocarbon dating of *c.* 8200 to 7950 B.P..

8.4 THE BOREAL FOREST

The transition from Pre-Boreal woodland to the Boreal forests is generally shown by a rapid rise in the abundance of *Corylus* and *Pinus* pollen (West, 1968). The order in which these two peaks occur seems to vary from site to site. This stage is generally marked by a fall in *Betula*. In time *Pinus* and *Corylus* gave way to a mixed forest of *Quercus*, *Alnus* and *Ulmus*. Characteristically Gramineae were at their lowest during this phase, *c.* 2% to 5% of the total dry land pollen sum. Sequences comparable with this have been described from many lowland sites in Britain, including the southern chalklands (Thorley, 1971; Waton, 1982). Such a 'normal' transition from the Pre-Boreal to the Boreal forests does not appear to fit the forest history described at Willow Garth.

At Willow Garth the Betula forest declined at c. 8800 B.P. and Pinus started to rise, as would have been the case in many pollen records. Instead of a succession of temperate forest tree species dominating the pollen spectra, Betula returned. The other taxa were present, indicated by both the pollen and macrofossil assemblages, but for some reason failed to shade out Betula. Indeed there is ample evidence of open land on which even Betula did not form a dense cover.

These data are most unusual and some explanation must be sought. Perhaps the dating of the site is completely at fault and that these deposits are much more recent than indicated. This does not seem likely as this section of the core had four radiocarbon dates, all of which were highly consistent with each other and with the date from the preliminary core, which was dated through a different laboratory. There is no indication of old carbonate error as the ^{13}C values were consistent at c. -29$^{o/oo}$. The climatic trends, with a warmer-than-present flora and fauna, are in accord with these dates. In short one could not hope for a better ^{14}C correlation and there is no apparent reason why the dating should be considered suspect.

There are 12 pollen samples within the Betula resurgence period (93 to 74 cm), which strongly suggests that this feature was not a quirk of under-sampling. There does not appear to be any disturbance of the sediment and it is therefore assumed that the palaeoecological evidence is reliable and an interpretation may therefore be attempted.

The first hypothesis is that trees could not grow on the Wolds because of adverse edaphic conditions. Whilst this might be a legitimate argument when applied to the steep scarp slopes of the southern downlands, the much gentler slopes of the Wolds can and do carry forest to this day. There is some evidence to suggest that there were thicker soils on the Wolds at this time (Cornwall, 1963) and this combined with the warm wet climate of the Boreal period would have been conducive to forest growth. Even Betula, which will root on the thinnest of soils and the steepest of slopes, was not shading out the ground flora. This suggests that the simple answer, that the trees could not invade this landscape, is inadequate.

There are three basic questions which must be answered:

Why was Betula not shaded out by the other trees?

Why did the Pinus peak decline so rapidly to be replaced by Betula?

Why was the open ground flora able to survive the expansion of the Boreal forest?

It would appear that the normal progression towards a Boreal forest was arrested by some form of disturbance. If this were the case the progression to a closed woodland would be expected to resume with the cessation of disturbance. That this did not happen for nearly 600 years suggests a prolonged or often repeated type of disturbance.

Again to take the most obvious form of disturbance first, let us consider the effect of fire. It has been suggested that the widespread peak of Corylus (Rawitscher, 1945), and other shrub species, which were often present at the start of zone V, was aided by forest fires. This argument has been put forward by a number of authors (e.g. Dimbleby, 1962; Keef *et al.*, 1965; Simmons, 1969). Experiments on American species of *Corylus* indicated that the genus was, to some extent, fire-resistant, although as Rackham (1980) noted this has not been proven for *C. avellana*. If the decrease in *Betula* and *Pinus* at Willow Garth at 93 cm had been due to fire one might expect a regrowth of *Corylus* rather than of *Betula* and an inwash layer of charcoal; neither of these is recorded.

These arguments have been applied to fires induced by man but they apply equally to natural fires. Rackham (1980) pointed out that in many areas fire would have been an inefficient way to destroy British woodlands as, with the exception of Pine forest, they do not burn well. It would seem unlikely therefore, that it was fire which was holding this community in a 'plagioclimax' state.

A further possibility is that this disturbance was caused by grazing animals. Coles and Orme (1983) suggested that beavers might have been of local ecological significance in the Boreal and Atlantic periods. This is an almost untestable hypothesis, and without further evidence must be placed on one side.

Other grazing animals, red deer, elk and wild cattle, may have exerted a strong influence on the vegetation, particularly near a watering-site. Willow Garth would undoubtedly have beenattractive to animals as it would have been one of the few permanent drinking holes on the Wolds. In America concentrations of grazing animals have been shown to create sufficient soil disturbance to allow Chenopodiaceae spp. to grow, although *Chenopodium* spp. were only recorded where burrowing animals had been active (McAndrews, 1966). The effect of excluding cattle from woodlands has frequently been shown to lead to an immediate increase in seedling regeneration (Rackham, 1980). The presence of grazing animals could certainly have helped the fen flora to diversify. Fen meadows have been shown to diversify under grazing and cutting regimes (Rowell *et al*., 1985).

Betula is a short lived tree and the 600 years covered by the previous sub-zone of WGP-5 would represent about 5 - 6 generations of birch trees. It is possible that once the forest was open the grazing pressure of wild animals could maintain local areas of grassland. However, this still does not explain the initial loss of the pine forest and the presence of so much timber in the deposit at this time.

An alternative hypothesis is that mesolithic man was exerting an influence on the local forests. At other mesolithic sites, where there must have been some forest disturbance in order to house a group and to provide them with timber for firewood, harpoons and spear shafts this is seldom discernible in the pollen record. This was probably the case at Star Carr (Walker and Godwin, 1954) and at Addington, Kent (Dimbleby, 1963). Therefore, the forest disturbance apparent at Willow Garth was probably on a larger scale.

It is worth considering briefly the current debate by archaeologists regarding the development of mesolithic communities. The view that the mesolithic was a rather static period in which stone tools were refined, but man made no attempt to domesticate stock or practice agriculture, has been challenged in recent years (Dennell, 1983). Traditionally it was held that mesolithic man did not make a great impact on his environment and that he lived within the forest structure, rather than shaping it to his needs. However, various workers have shown that, at least locally, mesolithic man could and did change his environment (Dimbleby, 1962; Simmons, 1981). Re-examination of 'neolithic' artefacts from the south-east England by Jacobi (1978) has led to many of these being re-identified as mesolithic. Not only does this illustrate the technological similarity between the two periods but it also provided evidence for a more widespread, and presumably larger, mesolithic population. Work by Care (1983) on the distribution of mesolithic hand-axes in south-east England supported the view that mesolithic sites were widely spread but tended to concentrate near the foot of the chalk outcrops.

Goudie (1977) suggested that Pre-Boreal forest closure led to the dissipation of the great reindeer and elk herds, forcing man to become a woodland hunter. This may have led to a desperate reduction in meat availability and precipitated the change in hunting patterns which led to the invention of the microlith. Dennell (1983) suggested that a similar food shortage, this time brought about by an expanding population and over-hunting, may have led to mesolithic man domesticating livestock and practising proto-agriculture. Roux and Leroi-Gourhan (1965) and Edwards and Hiron (1984) have discussed the possibility of such mesolithic activities and found evidence to support the view that mesolithic man was more than a mere hunter-gatherer. Indeed, far fom being scattered itinerant bands, some archaeologists consider the mesolithic communities to have been relatively settled and have started to refer to a 'Mesolithic Society' (Jacobi, 1978).

The traditional distinction between mesolithic man and neolithic man is that the former had neither pottery nor agriculture (e.g. Clark, 1936). As this distinction is eroded so there is controversy as to whether the boundary between the two periods is sharp, e.g. caused by invaders from the South-Eastern Europe overrunning the indigenous mesolithic peoples, or whether it was gradual, e.g. the natural development of a culture learning new skills through trading links with more advanced cultures (Renfrew, 1978; Dennell, 1983). The middle ground - an advancing neolithic culture melding with that of the resident mesolithic population - has been suggested by Bradley (1978). It would seem fair to state that the rigid distinction between the two periods is no longer adhered to and that it is seen as probable that mesolithic man was practising rudimentary livestock control and domestication. There is less clear evidence as to whether he was at this time cultivating crops.

Modern Palaeolithic hunter-gatherer economies rely on a knowledge of herd movements, the grazing habits of animals, and an understanding of the practical ecology of the local flora (Gould, 1982). Natural forest disturbance is a continual feature of woodland ecology. Lightning strikes, the senescence and falling of an old tree, and the subsequent wind blow causing further trees to fall, all would have been witnessed by the early hunters. They would also have witnessed the benefits of such disturbance.

Mellars (1975) estimated that the grazing improvement resulting from forest firing could lead to a x10 increase in the ungulate biomass that the land could support. This resulted from the numbers of animals increasing x5 and the average mass of each animal increasing x2. It is perhaps the increase in numbers that is the most significant as it offers the hunter a greater chance of a regular kill. P. Evans (1975) noted that under Boreal forest conditions Bos primigenius might have been phosphate deficient and consequently attracted to the phosphate-rich ash produced by forest fires.

Herein lies the reason for mesolithic man to fell the Boreal forests. The enclosing forest would have made hunting a difficult and uncertain lifestyle. To strengthen his chance of a kill he might have opened areas of land to concentrate the grazing herds. The modern day Palaeolithic peoples of Australia and Africa exhibit a sophisticated understanding of how to maintain a forest ecosystem to their own advantage. They have learnt the techniques through observing natural phenomena, and then used their acquired knowledge to shape the vegetation.

If this was happening at Willow Garth the evidence would suggest that fire was not used to clear the forest. Man may instead have been felling patches of woodland to improve the grazing potential, and therefore the carrying capacity of the land.

The presence of a timber rich layer in the core at 91 - 77 cm which is primarily composed of wetland species, but also contains fragments of Quercus, would support such an hypothesis. Although the wetland taxa may have simply collapsed into the fen, it is unlikely that Quercus was growing on the fen itself and so the presence of Quercus timber may indicate forest disturbance on the drier slopes of the valley. The fragments (up to 6 cm x 1.5 cm x 1.5 cm) were from mature timber, not twigs, as it is only possible to identify wood which shows considerable secondary thickening.

At most sites where there was clearance for agriculture, tree stumps were uprooted to allow ploughing, rendering the soil susceptible to rapid erosion. In such circumstances there is likely to be an increased mineral input to the site with a consequent fall in the organic carbon content of the sediment. However, subsequent regrowth following forest disturbance by a form of coppicing or ring-barking, could help to explain the continuing presence of leaves and bud scales whilst pollen and fruits were scarce. The illustration of a tree being felled using a stone axe (Iversen, 1956) is particularly interesting as it suggests that the coppiced stool of a tree would have been about 80 cm high. It would have been an enormous amount of work to clear these stumps and so it is likely that they were left in the ground. The coppicing would not result in the land surface being broken and hence there need be no marked increase in the rate of erosion.

However, what might be expected is a layer of timber fragments produced from the chips of wood produced by axe cuts and the subsequent logging up of the wood. A woodland coppiced by axe will have a mat of timber fragments and brash littering the ground surface; these might well be washed down into a nearby pool. The effect of this would be to increase the organic carbon content of the sediment, the reverse of the trend normally associated with clearance horizons for agriculture.

Such an hypothesis is one possible explanation of the available evidence from Willow Garth, where there is an increase in the organic carbon content of the deposit from 8% to 31% between *c.* 8650 B.P. and 8300 B.P.. Thereafter the organic carbon content falls back to *c.* 7%.

Coppicing, or ring-barking, would produce an unshaded area in which vigorous grass and herb growth would provide improved summer grazing. The new shoots from the cut stools would provide young leaves and bark which would also be eaten either by grazing animals or by man. The cambium of *Sambucus* and *Tilia* were used as a starch-rich staple as late as mediaeval times (Dimbleby, 1967). The weed species present at this time suggest rough pasture with some degree of continuing disturbance. It may be that mesolithic man would have realised that to turn the soil surface with a digging stick helped weeds such as *Chenopodium album*, *Atriplex*, *Polygonum lapathifolium* and *Aphanes* to germinate. Seeds of these plants are thought to have been used as food sources of starch and protein by hunter-gatherers (Glob, 1965; Dimbleby, 1967). Man may therefore have made some effort to encourage the growth of these species. This may also have been the case with *Rubus idaeus*, which is very easy to strike from cuttings. Seeds of *R. idaeus* were found in two levels from this period.

The presence of large Gramineae pollen (length >44 µm) in four consecutive samples from this biozone is particularly interesting. Known montane or halophytic species were completely absent from these levels and the climatic regime suggested by the other taxa present indicates that the grasses specially adapted to xerophytic and coastal conditions are unlikely to have survived. Given that wild grasses, when subjected to environmental stress, or at the edge of their distribution, might produce abnormally large pollen grains (sensu Jones and Newell, 1948), it would be possible for these grains to be derived from wild type grasses. There would have to be a relatively high percentage of such grains as 8 out of c. 400 are of an extreme size. Less than 1% would be predicted for this size range of 46 - 52 µm even amongst the largest wild type grasses (Beug, 1961). It might also be expected that if these were at the positive extreme of a normal distribution, that this distribution would be seen by the representation of most of the other size categories in the size histogram. That the largest, presumably the rarest, size of grain of a normal distribution has been found more than once suggests the sample size is big enough for other size categories nearer to the modal peak to be represented. This does not appear to have been the case, as at 87 cm there was only 1 pollen grain in the size classes from 34 - 50 µm. In the other levels there was none in the classes from 34 - 44 µm at 91 cm, and at 93 cm there was a single grain in the size range between 36 and 44 µm (Fig. 7.10). If these grass pollen grains were simply large forms of species already present, one would expect them to form the tail of a normal distribution of pollen sizes. That they apparently exist as the representation of a species different from those previously recorded, would lend support to the view that there had been some environmental change.

Despite their large size (48 - 52 µm), and broad annular width (11.5 µm), the grains do not appear to be Triticum type. The annulus is not broad enough in relation to the pore size for them to be of this group. This of course assumes that the very early Triticum grains were similar to those from the neolithic and Bronze Age periods. These grains have been tentatively identified as Hordeum or Avena; the comparison with Avena reference material provided the best match but identification to that level is somewhat uncertain. If these grains were from Hordeum or Avena it is possible that the caryopses would have been collected by mesolithic man, and like the other taxa of disturbed ground, the growth of these large seeded wild grasses might have been encouraged by deliberate soil disturbance.

The selection of Willow Garth for such activities is not surprising as the standing water would have been the natural focus for human activity. The valley bottom of the Great Wold Valley probably contained a string of such fens joined by the Gypsey Race. This would have provided an extensive habitat in which to hunt and fish, and at the same time offer nearby sandy soils for proto-cultivation and the establishment of camps. Elsewhere in the Great Wold Valley the mesolithic sites of Bessingby (Earnshaw, 1973) and Burton Fleming (unpublished research by C. and E. Grantham of Driffield; artefacts from a mesolithic flint factory are in their private collection) both lay on sandy deposits in the valley bottom. As can be seen from the diagram of drift deposits (Fig. 2.2) there is an extensive area of sandy deposits immediately to the south of Willow Garth. It has been suggested that the sandy soils supported Pinus until the first phase of clearance. If the people at this time preferred to live on such soils then these trees would be the first to be felled. As Pinus does not coppice there would have been no opportunity for the tree to regrow until the site was abandoned.

The apparent reason for the regrowth of Betula after the decline of Pinus is that it was occurring as a secondary forest tree. Fraxinus excelsior, another tree which Rackham (1980) suggested as being characteristic of secondary forest, was slow to expand from its southern European refugia. The pollen maps of Huntley and Birks (1983) suggest that F. excelsior did not reach Britain in any numbers until c. 6000 B.P.. Although F. excelsior was recorded for the first time in this biozone, it is likely that it was a relatively rare tree. The lack of competition from F. excelsior and the deeper soils present on the Wolds during the pre-neolithic period (Cornwall, 1963), combined with the immense capacity for seed dispersal of Betula, would have favoured Betula as the dominant secondary forest coloniser at this time.

8.4.1 The Duration of Disturbance

Late in sub-zone i and throughout sub-zone ii of WGP-5 there is an apparent decline in the diversity of species represented in the pollen spectra. In these levels, at 84 cm and at 72 cm, the lack of species diversity may have been caused by the rise in the Betula curve. The pollen values of this taxon rose to 68% at 84 cm and 55% at 72 cm. There was no corresponding rise in the Betula macrofossils and so this increase may have been taking place beyond the fen margin. If the model proposed, i.e. of mesolithic forest disturbance with Betula occurring as a fen edge and secondary growth tree, is accepted, then the loss of species diversity and the sudden increase in Betula pollen would be consistent with an abandoned clearance area being allowed to revert to secondary growth.

This would suggest that two clearance phases are shown, the first from 93 to 85 cm (c. 8800 - 8600 B.P.) and the second from 80 to 75 cm (c. 8400 - 8250 B.P.). These were longer clearance phases than originally suggested for neolithic Landnam phases (50 -100 years) (Iversen, 1941) but are more in accord with the estimates by Buckland and Edwards (1984) and Sturludottir and Turner (1985) of > 250 years. It is of interest to note that the organic carbon content of the sediment drops from 31% at 77 cm to 7% at 74 cm. If the suggestion made earlier, that the woodland practice was one of coppicing rather than clearance, is correct, this might indicate that the last phase of active clearance was at 77 cm (c. 8350 B.P.) and that afterwards grazing kept the forest open for a time. The rapid migration of the DECORANA curve towards a more characteristic Boreal woodland suggests that a mature woodland was gradually regenerating.

If modern clearance of woodlands is observed Betula will frequently be seen to form dense secondary growth. A freshly cleared area is quickly covered by Betula seedlings. The young trees grow rapidly, forming a dense stand of immature trees. Species less well adapted to rapid colonisation, e.g. Quercus, will arrive in due course and their seedlings are often to be found in the understorey of such woodlands. In these woodlands the Betula are of a similar age and there is a tendency for them to become senescent together. This gives the young Quercus a chance to grow through to the canopy. It is in this period that the dominance of Betula regrowth is broken. As the lifespan of birch trees ranges from 80 to 120 years (Rackham, 1980) this change may be expected to take place c. 100 to 140 years after regeneration started. Local modern analogues for such an environment can be seen at Epworth Turbary, Isle of Axeholme, (Lincs. Nats. Trust Reserve) and the Warter Estate on the Yorkshire Wolds. At both sites, woodland clearance took place at the beginning of this century and the birch forests are just beginning to give way to Quercus woodland.

This would conform reasonably well with the fossil data from Willow Garth. If the Betula regrowth started at 74 cm it would be c. 100 years before Quercus and other trees started to assert their presence in the canopy. This would be at about 72 cm and it was from this level that the DECORANA results indicated a pronounced change in the forest ecology. The phase of regrowth within the main disturbance phase from 8800 to 8600 B.P. may still have been influenced by man or animals effectively prolonging the regenerative cycle.

In sub-zone ii of WGP-5, Pinus returned as an important component of the pollen spectrum, perhaps indicating that Pinus was regrowing unhindered on the sandy soils and that the settlement had moved from this site.

The insect and propagule assemblages indicated the presence of areas of open ground right up to the hiatus at 67 cm. These suggest that the forest cover was not total and that, even 300 years after what appears to be the abandonment of the site, patches of grassland remained. The pollen output of these areas was all but obscured by the prolific pollen production of Betula, Pinus and Corylus.

It is possible that the focus of man's attention had moved to another site within the valley and that the scale of interference at Willow Garth was much reduced. However, it is unlikely that man would totally abandon a site which suited his hunting requirements so well. The duration of this phase of little disturbance is not known as there is a discontinuity in the pollen record from c. 8000 B.P. to 4000 B.P.. The evidence of known late-mesolithic occupation sites at Bessingby, Burton Fleming and Kilham (Earnshaw, 1973; Manby, 1976), and the exceptionally high density of neolithic remains around Rudston (Manby, 1975), sites which are all within an easy walking distance of Willow Garth, suggests that intermittent disturbance might be expected throughout the remainder of the mesolithic and early neolithic periods.

8.5 THE SUB-BOREAL

8.5.1 Biozone WGP-6 (67 - 53 cm), (c. 4150 - 3600 B.P.)

Sediment

The suspected hiatus passes through 67 cm and this level seems to represent something of the floras of above and below. Only slight vertical mixing at the time when deposition recommenced and an uneven surface, over the 7 cm wide area which was sampled would have been sufficient to cause a rather confused and confusing level. Consequently, it is probably best to leave it out from the present discussion.

The sediment accretion of this biozone was of similar material to that of WGP-5. The hiatus, which is not visible to the naked eye, is marked by a decline in the organic carbon content, from 7% to 4% by mass. This may be attributable to the inwashing of some fine sands. There were no coarse sands or gravels and no coarse organic detritus in this sample. Had the sedimentary discontinuity been the product of stream erosion more evidence of the sediment load of the stream might have been expected. That more sand did not accumulate during the period of the hiatus suggests a stable regime in which soil erosion from the surrounding slopes and flooding did not take place.

Biozone WGP-6

Vegetation

The mosses making up the sediment above the hiatus included: Rhizomnium punctatum, Calliergon cuspidatum, *Drepanocladus revolvens* and *Amblystegium riparium*, all of which are mosses of fens and other wetland environments.

The insect fauna was very similar to that below the hiatus and included the dry grassland indicator *Philopertha horticola*.

The aquatic fauna and the wealth of aquatic flora represented by propagules suggest a rich weedy pool environment. In addition to those aquatic taxa listed in the previous biozone, *Alisma plantago-aquatica* and *Baldellia ranunculoides* were recorded. The fen flora was as diverse as in previous samples and noted for the first time were: *Lycopus europaeus*, *Berula erecta*, and *Thalictrum flavum*. Absent from this flora were Orchidaceae and *Polemonium caeruleum*.

The first occurrence of fruits of *Corylus avellana* and *Crataegus monogyna* corresponded with a peak of *C. avellana* of 28% at 62.5 cm. Another arboreal taxon which was noticeably more abundant in this biozone is *Alnus* which attained a peak of 20% at 60 cm. Considering that this is a wetland taxon which is often thought to be over represented in valley deposits, this was a very modest peak. *Quercus* reached a maximum of 5.4% of the dry land pollen sum, whilst *Pinus* was reduced to 3%. *Tilia* appeared for the first time in this zone, attaining a maximum value of 2.5% at 56 cm. The significance of this peak is discussed in section 8.6.

This arboreal flora would appear to represent the remnants of an Atlantic forest association in what was a predominantly open landscape. The presence of weed species associated with arable land is noticeable in both the pollen and macrofossil records. The fruits of *Stellaria media*, *S. alsine*, *Polygonum convolvulus*, *P. lapathifolium*, *P. aviculare*, *Chenopodium album*, *Brassica rapa* and *Anthemis cotula* were all indicative of disturbed land. In the pollen record, in addition to the taxa named in the macrofossil assemblage, *Plantago lanceolata* increased steadily from 11.4% at 52 cm and there is the first regular occurrence of cereal type pollen with sizes up to 58 µm long with a 17 µm annulus, as found at 60 cm. This was tentatively identified as *Triticum* type pollen. Also present were species indicative of open grassland, e.g. *Centaurea nigra*, *Plantago* spp., *Bellis* and the fruits of *Prunella vulgaris*. As Behre (1981) stated, the boundaries between cultivated and non-cultivated areas were probably vague. It is probable that patches of rough grassland existed for grazing in a mixed landscape of small cultivated plots, coppiced woodland, fen and chalk grassland.

The *Ulmus* decline, if there was one, went unrecorded as no *Ulmus* pollen was found in any of the previous biozones. In this biozone the late date, the presence of agriculture and the sporadic presence of *Ulmus* at <1% suggests a post *Ulmus*-decline age. This leaves us no wiser as to whether the elm had ever been sufficiently common on the Yorkshire Wolds to have suffered a decline.

Biozone WGP-6

Climate

The recommencement of deposition, after what is thought to have been a 4000 year standstill in sediment accretion, might suggest a net increase in the water input to the site. As suggested previously the controlling factor in sediment accumulation may have been the seasonal flooding of the Gypsey Race. If this were so then there was a sufficient increase in the flow of this stream to cause flooding. This may have come about through increased precipitation, or from impeded drainage lower in the valley.

Teucrium botrys, *Moehringia trinervia* and *Eupatorium cannabinum*, the most temperature sensitive plants recorded at the end of the previous biozone, were absent from this and later biozones. These species may have been occurring at the northern extreme of their distribution and are missing from this assemblage because of a slight climatic deterioration. Another species present in the later samples of WGP-5, but which went unrecorded in WGP-6, was *Sanguisorba officinalis*. This taxon has a distinctly thermophilous modern distribution, extending only as far north as Berwick (Godwin, 1975).

A period of decreasing temperatures and unchanged precipitation would result in a net increase of water in the rivers and fens, a model which would be supported by the evidence from Willow Garth of an expansion of the wetland area and the renewed peat growth recorded in this biozone.

Biozone WGP-6

Relative dating

This biozone appears to correspond to the Sub-Boreal period, zone VIIB of the Flandrian. The timing of this would correspond well with the end of the hypsithermal advocated by Lamb (1969), which lasted between 6950 B.P. and 4350 B.P..

8.6 *TILIA*: A FOREST DOMINANT, OR A MISUNDERSTOOD TAXON ?

Considerable interest has focussed on the Atlantic *Tilia* peak which is to be found in many pollen diagrams from lowland Britain (e.g. Godwin, 1968; Girling and Greig, 1977 and Thorley, 1981). The peak has not been found in all diagrams and there is some debate as to the extent of *Tilia* cover and dominance (Moore, 1977). The relevance of such a peak was underlined by the assertion of Pigott (1969) that *Tilia cordata* was probably one of the most dominant trees in many lowland forest associations before anthropogenic clearance. The ancient *Tilia* woodlands of South Yorkshire, Derbyshire and Essex have all been suggested as remnants of a once widespread forest type (Peterken, 1981; Rackham, 1980). Work by Turner (1962), investigating the post-interference regeneration of *Tilia cordata*, indicated that this species was at a competitive disadvantage to secondary woodland taxa, e.g. *Fraxinus excelsior*, *Acer pseudoplatanus* and *Ulmus* spp.. Turner went on to suggest that the decline in *Tilia*, often an event linked to the *Ulmus* decline, or occurring shortly afterwards, was also an anthropogenic event. These arguments would support the hypothesis that *Tilia cordata* was once a widespread dominant of lowland forests. The palynological evidence to support such a claim is somewhat equivocal.

The greatest problem in interpreting a *Tilia* curve in a pollen diagram is the suspected under-representation of *Tilia* (Andersen, 1973; Bradshaw, 1981a). *T. cordata* produces large quantities of pollen (Godwin, 1975), but the grains are sticky, an adaptation to entomophily, but not conducive to efficient anemophily. The grains have a tendency to clump and fall to the ground close to the source of origin. Such a local distribution has been recorded repeatedly (Andersen, 1973; Bradshaw 1981a) and again in the present study.

In order to compensate for this apparent under-representation weightings may be applied which reduce the significance of some taxa (e.g. Betula and Pinus), whilst increasing the proportion of Tilia. Such calculations must be undertaken with caution, otherwise spurious results will be obtained. Weightings will work more efficiently for common species than for relatively rare taxa. If there is an abundance of an over-producing taxon the long range component of that taxon is lost amidst the local production. The error of this component is then further reduced by dividing by a weighting factor greater than one. By contrast, if there is a rare under-producing taxon, the possibility of a relatively high percentage of that pollen being of long range origin cannot be discounted. If this taxon is then divided by a weighting factor of less than one the potential error from chance long range dispersal is proportionately increased.

In other instances some authors have chosen to exclude certain taxa from the pollen sum. Alnus is frequently omitted (Janssen, 1959; Scaife, 1980; Waton, 1982). However, there is some evidence that the current wetland distribution of Alnus is a product of habitat loss, and that Alnus may have been a more general forest component during the Atlantic period (Praglowski and Wenner, 1968). Salix and Betula have, on occasion, been excluded from the pollen sum on the grounds that they may have been growing on the wetland. Certainly this is possible, but they may have been an important and characteristic component of the woodland flora.

Salix pollen is often assumed to be derived from wetland species although some shrub Salix species, S. capraea and S. cinerea, may flourish in secondary woodland growth or in a shrub understorey in relatively open forest. Betula of course can be found in many associations, particularly with Quercus petraea (Peterken, 1981) and it should not be assumed that the pollen is locally derived. Modern pollen rain studies indicate Betula pollen to be extremely well dispersed, maintaining high concentrations over several hundred metres (see section 6.7.2).

Corylus is another taxon which has been excluded from the pollen sum because it is thought to be over-represented. This however is not a just criterion for excluding it as Corylus is often an important woodland component. Furthermore, under the management of mesolithic and neolithic man it may have been coppiced and nurtured. Thus to remove it from a pollen sum may be to overlook a key woodland component.

In the study of Hampstead Heath, London, Corylus, Salix and Alnus were all excluded from the pollen sum (Girling and Greig, 1977). The commonest pollen type at this site was Quercus, which could have been growing in a mixed woodland assemblage with any, or all, of these excluded taxa. Tilia was then found to total 33% of the dry land pollen total. This can be recalculated so as to include all taxa and Tilia then accounts for 20% of the total dry land sum.

> " There is some English evidence also for natural occurrence of T. cordata in fen margin woods. "
>
> (Godwin, 1975 p. 163)

This might suggest that Tilia would be locally common in wet places where the rich mull humus soils on which it thrives (Rackham, 1980) are most likely to occur. Rackham (1980) observed that Tilia was a common fenland tree until the draining of the fens in the last century, and suggested that the present distribution, as a dry land forest tree, is as much a product of habitat destruction as ecological preference. Tilia might, therefore be regarded as a species likely to be locally over-represented around a boggy area and not necessarily having a homogenous distribution throughout the forest. If Alnus, Salix and Corylus are to be removed from the pollen sums of small basins, e.g. Hampstead Heath, there would be some justification in advocating the exclusion of Tilia also.

Tilia has been demonstrated to be a highly durable pollen grain, a quality which may be attributable to the high (14.9%) content of sporopollenin in the exine (Havinga, 1967). Tilia has, however, been experimentally shown to be susceptible to perforation corrosion. Even so, it was more resistant than most pollen types (Havinga, 1971). The process of pollen decay will vary from species to species, and also according to the preserving medium, but Tilia was consistently found to be amongst the most durable grains tested. The experimental conditions used by Havinga did not take into account pressure processes, abrasion, distortion and crumpling, factors which Cushing (1967) suggested as likely to accelerate the process of decay. The resistance of sporopollenin to pressure forces may be the determining factor preventing decay. Thus the 14.9% sporopollenin content of Tilia may be a more efficient shield against such processes than the 5.1% sporopollenin content of Quercus. This might explain why Tilia has frequently been recognised as a selectively preserved taxon (Godwin, 1975), whereas such records for Quercus are rare.

It is not surprising to find that some of the deposits in which Tilia appears at its most abundant are those in which there is a low concentration of pollen and selective preservation is suspected. An example of this would be the buried soil beneath Kilham Long Barrow where Tilia was found to be the commonest arboreal taxon (Evans and Dimbleby, 1976).

In shallow depositional environments such as those of Epping Forest (Baker et al., 1978), Hampstead Heath (Girling and Greig, 1977), Oxborough Wood (Bradshaw, 1981b) and indeed Willow Garth a course of events as described below might indicate how a peak of Tilia could be found through selective preservation, in what appears to be a richly polliniferous deposit.

If there are a series of standstill levels, each one lasting for a few years, in which oxidation of the surface layers destroys the organic matter as it is deposited, and the oxidation also destroys all but the most resistant pollen grains then a depauperate flora might be expected. However, if such periods of oxidation were interspersed with brief periods of peat formation in which the upper layer of oxidised peat became incorporated with the new peat growth, or the stratification was too fine to be separated during palynological processing, then a mixed flora would result: one in which the selectively preserved taxa were combined with the 'normal' pollen influx for the deposit. This would have the effect of exaggerating the selectively preserved taxa and yet maintaining the full diversity of 'fragile' species taken to indicate conditions of good preservation.

A test for this model would be to compare sedimentsfrom deep water bodies and shallow pools. If this hypothesis were not to be refuted a consistent trend of higher Tilia values from the shallow water deposits than the deep lakes would be expected. A comprehensive survey of sites to investigate this is beyond the scope of this thesis, but four sites are considered briefly.

An interesting pair of sites are those of Oxborough Wood and the 20 km distant Hockham Mere. At Oxborough Wood, a small hollow within the wood yielded a mid-Flandrian pollen sequence with a maximum of 20% Tilia pollen (Bradshaw, 1981b). Jacobson and Bradshaw (1981) suggested that small hollows would yield more accurate results for local variations in woodland composition than the deposits from large water bodies. At Hockham Mere Tilia reached a maximum of 5% of the dry land pollen sum. Either the Tilia pollen was not as well represented in the lake, or there had been selective preservation of the woodland deposit, or Tilia was not a wide spread dominant. Bradshaw (1981b) acknowledged that selective preservation might have biased the data and presented a table of pollen preservation from which it could be seen that preservation was generally poor. These would be the conditions in which selective preservation of Tilia might be suspected.

> " Small sites are particularly susceptible to periodic dessication and subsequent deterioration of pollen."
>
> (Bradshaw, 1981b p.952)

It is pertinent to note that the sites most often quoted as having high Tilia percentages, e.g. Epping forest (Baker *et al.*, 1978), Hampstead Heath (Girling and Greig, 1977) and Oxborough wood (Bradshaw, 1981b) are, or were, all small, shallow woodland sites in which there was evidence of standstill levels and levels of poor pollen preservation. Even the pollen record from the larger alluvial site of Shustoke (Kelly and Osborne, 1968) may have been subject to selective pollen preservation; a phenomenon likely to occur at a site which relies on periodic flood events to maintain anaerobic soil conditions. These sites might be considered unsuitable for the specific study of a highly durable pollen grain such as Tilia, particularly when the species is thought to have grown in the wetter areas of a wood.

A further point to be considered is the mode of transport of Tilia grains into a deposit. The data which indicate that Tilia was an under-represented tree have come from the trapping of airborne pollen grains. If however, the pollen was also being dispersed by surface water movements and incorporated into sediments through stream inputs to a catchment, this could substantially alter the depositional record (Peck, 1973; Bonny, 1976). Tilia is not only a prolific producer of pollen, much of which drops staight to the forest floor, but because of its high durability it may not decay as quickly as other pollen types on the soil surface and so the slope-washed pollen might be Tilia-rich.

Even when considerably decayed, or partially obscured by detritus on a slide, Tilia is a highly recogniseable grain. This may lead to over-recording by the palynologist, who may not be able to recognise another pollen type when equally damaged or hidden.

8.6.1 The Status of Tilia on the Yorkshire Wolds

Tilia first occurred in the Willow Garth record at 67 cm, the level of the hiatus. Thereafter, Tilia occurred in four consecutive samples attaining a maximum value of 2.5%. Tilia then disappeared from the pollen record, apart from two grains at 42 cm, until 36 cm where it reappeared as a regular component (c. 0.25%) of the dry land pollen sum. It finally diappeared at 10 cm.

The highest influx of 3.4 grains cm^2 y^{-1} came at 24 cm, although the Tilia concentration at this point was only 288 grains g^{-1}, less than half that of the maximum concentration in the core. This maximum, 757 grains g^{-1}, and the maximum Tilia percentage coincide at 60 cm, which was a level of low total pollen concentration, c. 40,000 grains g^{-1}. The samples from 57 to 67 cm could represent Tilia rich woodland. The timing of this peak at c. 3750 B.P. - 4180 B.P. would correspond well with the Tilia peaks recorded from many other pollen diagrams (Godwin, 1975). The 2.5% total pollen can be transformed to an arboreal value of 8.2% total tree pollen, and if Corylus, Salix and Alnus are excluded this is further increased to 12.5%. If the absolute data are transformed using the weightings (R-rel) obtained from the modern analogue study, 3 of the five levels suggest woodland canopies of >25% Tilia, with a peak of 33% at 60 cm.

The value of 2.5% for a Tilia maximum is the same as that recorded by Turner (1962) from Thorne Moor, S.Yorks. At Thorne Moor the Tilia pollen curve was observed to decline independently of other tree taxa present. This was interpreted as the selective felling of Tilia, or the destruction of a pure stand of Tilia (Turner, 1962). Apart from Willow Garth the only other data available for the Wolds are those of Evans and Dimbleby (1976) from Kilham. At Kilham they recorded 15.5% Tilia in a buried soil pre-dating a barrow constructed c. 4800 B.P.. This early date and high value for Tilia might reflect that Tilia was growing on the Wold tops. If this were the case the pollen was being derived from a local source at Kilham, and hence might explain the higher Tilia values from this site than those recorded from Willow Garth.

Alternatively, the clearance of Tilia-rich forests had reduced the forest cover between 4800 B.P.and 4180 B.P. and so the later record at Willow Garth had missed the Tilia peak. The pollen record from beneath Kilham Long Barrow shows that clearance and two phases of cultivation had already taken place prior to the construction of the barrow. One inference might be that as clearance progressed so the yield of Tilia pollen declined and that the record of the forest in WGP-6 represented fragments of a once extensive cover. This would certainly fit with the low forest pollen input to Willow Garth at this time and evidence of local agriculture. *Tilia* would appear to have been an important component of the remaining forest and there is some evidence that selective felling of *Tilia* took place at *c.* 3750 B.P..

Such an hypothesis is in close accord with the results of Waton (1982) at Winchester and Rimsmoor, Turner (1962) at Thorne Moor and Bradshaw (1981b) at Oxborough Wood, Norfolk.

However, there is an alternative hypothesis that should be considered. The maximum value for *Tilia* pollen (no macrofossils were found) at Willow Garth was 2.5 (+2.5 / - 1.3)% of the dry land pollen sum.. The error bars appear large because the pollen type is relatively rare and they underline the necessity for caution when interpreting the data of rare taxa. Therein lies the crux of the argument: what confidence can be placed on predicting degrees of forest dominance for a taxon which seldom exceeds 10%, in any pollen assemblage, when count sizes are not sufficient to minimise the error bar of a 95% confidence limit?

As shown in the preceding section, the 2.5% value of *Tilia* can be transformed, by widely used methods, to indicate a canopy presence of 33% in the local woodland cover. Yet this relies on a model with serious constraints, the problems of which are discussed in section 8.9, but the most serious of which relies on the *Tilia* occurring within 20 m of the site of deposition. The *Tilia* pollen in the modern analogue study declined to less than 1% at 50 m from the nearest *Tilia* stand. Of course, if the *Tilia* forest predominated, the regional pollen component might be expected to lessen the decline of this curve. However, the low total forest pollen input indicates a relatively open landscape at this time and it might therefore be expected that the modern analogue is a reasonable representation of the pollen representation from an isolated block of *Tilia*-rich woodland. This would imply that *Tilia* was growing within 50 m of the deposit, which is not an unreasonable assumption as it has already been stated that *Tilia* grew in the fringing woodlands of fens. It is a little surprising therefore to find no representation of *Tilia* in the macrofossil assemblages. *Tilia* fruit can and do preserve (Wright and Wright, 1947) and as acorns, timber, leaves and bud scales of *Quercus* were found from these levels one might have been expected to find some trace of *Tilia*. North Ferriby, and Shustoke (Kelly and Osborne, 1964) are the only records of *Tilia* fruits listed by Godwin (1975). It is perhaps surprising that more macrofossils of this tree have not been recorded.

How then should the *Tilia* peak of Willow Garth be interpreted ? The answer is that it may not be possible to interpret these data with any accuracy. Firstly, the peak occurred within a section of the core which, although showing excellent diversity and preservation, has a low concentration of pollen. Under such circumstances the effects of selective preservation may be increased. Secondly, it has been suggested that peat formation at this site may have been related to the periods of flooding by the Gypsey Race. The effects of an inwash of pollen, from seasonal bank overtopping, on the proportions of durable pollen types is unknown. It could be reasonably suggested that this water could be dispropotionately rich in *Tilia* pollen due to the earlier selective preservation of pollen on the woodland floor. Thirdly, the possibility of standstill levels might also have induced selective preservation and yet have left an apparently polliniferous, species-rich assemblage as discussed above.

The evidence from Kilham must be treated with even greater caution as the assemblage comes from a mineral soil horizon in which it is most probable that selective preservation took place (Jacobson and Bradshaw, 1981).

Having put the case against the validity of the Tilia pollen records it must be recognised that for Tilia to occur so often in areas from which it is now absent it must have been more widespread than at present. The argument above is designed to illustrate that the interpretation of rare taxa must be approached with caution and that until more is understood about the transport of Tilia pollen to, and its preservation in, sediments, it is rash to make assertions about the possible dominance of this taxon.

The only conclusion which may be safely drawn from these data is that Tilia was a component of the mid-Flandrian forest which grew on parts of the Wolds and that the abundance of this taxon was probably greater than its present distribution suggests. The widespread clearances of the Bronze Age greatly reduced the forests in which Tilia grew and there is no evidence to suggest that it was able to become re-established on the Yorkshire Wolds in any great numbers.

8.7 THE LATE FLANDRIAN

8.7.1 Biozone WGP-7 (51 - 35 cm), (*c.* 3600 - 1200 B.P.)

Sediment

Within this biozone there lies a change in the sediment stratigraphy from moss peat to a mossy lake mud. This sediment change at 51 to 48 cm probably reflects a hiatus in the pollen record which is estimated to have lasted from 3400 to 2120 B.P.. The sediment differs in texture and pH above the discontinuity, suggesting some alteration in the depositional environment and some change in the hydrological input to the sediment. There is no marked variation in the pollen spectra in the samples spanning this boundary, which suggests that local land use had not changed radically in the periods immediately before and after the hiatus.

Biozone WGP-7

Vegetation

Quercus pollen was constant at 4% to 6%, *Alnus* was declining to *c.* 4% and *Tilia* was present at <1%. The percentage pollen of arboreal taxa was less than 20% throughout this biozone, indicating that extensive clearance had taken place. The occurrence of *Cerealia*, *Aphanes*, *Centaurea cyanus* and *Anagallis* pollen suggests arable cultivation. The *Cerealia* pollen grains of these levels are up to 66 µm in size; grains as large as this may be of *Secale cereale*.

The macrofossil record reflects the presence of agricultural land with a similar range of disturbed ground species including *Rorippa islandica*, *Urtica urens*, *Fumaria* *officinalis*, *Euphorbia exigua*, *Stellaria media* (12%), *Brassica rapa* and *Anagallis arvensis*. An unidentified pulse was found at 44 to 40 cm; it was not a wild type legume but identification was uncertain. The occurrence of a left first molar from a domesticated cow at 48 to 44 cm indicates that stock animals were being kept at this time. Whilst the exact location of the tooth may have come about through its being washed into the deposit, the fenland flora at this time has the appearance of a rich fen meadow, an association which would nowadays need grazing or mowing to maintain its diversity (Wheeler, 1980c).

A peak of Cruciferae, with a maximum of 19% of the dry land pollen sum, was a characteristic feature of this biozone. Fruits of a wide diversity of cruciferous plants were recorded from these levels, but none was strikingly common. Had *Cardamine*, *Nasturtium aquaticum* or *Nasturtium microphyllum* been the cause of the pollen peak an abundance of their fruits might have been expected. An alternative habitat for the Cruciferae would have been as weed species of arable fields. Weedy field conditions would certainly be consistent with some of the other taxa present. However, the size of the crucifer pollen peak is much higher than that of any of the other weed species and might reflect the local cultivation of one of this family.

Chalk grasslands were also in evidence in this biozone with fruits of *Linum catharticum*, *Prunella vulgaris*, *Papaver* and *Papaver rhoeas*. There was also the pollen of *Sanguisorba minor*, *Gentianella*, *Centaurea scabiosa*, *C. nigra* and *Dipsacus*.

The presence of large numbers of mollusc testa was probably due to the increasing alkalinity of the deposit during this biozone. Amongst the molluscs were open ground species, e.g. Vallonia excentrica and Vertigo pygmaea. The other molluscs were derived entirely from the fen and fen margins. These included species indicative of slow or still, weedy waters, e.g. Armiger crista, Valvata cristata, Planorbis spp. and Bithynia tentaculata. Other taxa such as Lymnaea spp., Pisidium personatum, Succinea putris and Anisus leucostoma would have lived in almost any wetland conditions and could survive periods of dessication. There was an increase in mollusc diversity throughout this biozone, but this could be due to the selective preservation of the thicker shelled species in the lower, more acid, levels of the zone.

The insect record contained Philopertha horticola in the samples from 52 to 48 cm but this species was absent thereafter. Other species present included the terrestrial beetles Apion spp., Geotrupes and the shield bug, Elasmuchea grisea. Other than these the fauna was of the aquatic and fen families Dytiscidae, Hydrophilidae and Hydraenidae.

The change in sediment may have been associated with the Gypsey Race carrying an increased burden of silt. Such could come about through the ploughing of land within the watershed. This would correspond with the overall environmental image of an open landscape in which widespread deforestation and arable cultivation were taking place. The agricultural practices may have included the cultivation of pulses, crucifers and cereals, e.g. Triticum and Secale cereale. Grazing cattle were kept and these may have contributed to maintaining a diverse fen and chalk grassland flora.

Biozone WGP-7

Climate

The disappearance of Philopertha horticola from this deposit was not due to habitat loss as there is abundant evidence of grassland environments throughout these levels. This would suggest that the climatic requirements of this insect were not being met by the climate of this biozone. Sanguisorba officinalis was again absent from these levels, which would support the argument that the climate was as bad as or worse than that of the previous biozone. The cultivation of Secale cereale in preference to Triticum was suggested by Goudie (1977) as being a response to a deteriorating climate during the late Bronze Age and Iron Age.

Biozone WGP-7

Relative dating

Evidence of a relatively cool wet climate suggests that this was part of the Sub-Atlantic phase, zone VIII of the Flandrian.

8.7.2 Biozone WGP-8 (34 - 0 cm), (c. 1200 - 0 B.P.)

Sediment

Before a discussion of the flora and fauna of this biozone can be undertaken, it is necessary to examine the occurrence of a stratum of chalk fragments which appears to form a continuous, but loose, scatter across the entire area stratigraphically surveyed at Willow Garth. This layer which was present in every core at c. 30 cm down the stratigraphy was c. 1 cm thick, composed of flat chalk, and some flint, pebbles of up to 3 cm^2. There were no accompanying sands and gravels. The chalk fragments did not form an obvious boundary between two different types of deposit and, furthermore, the organic mud on either side of the chalk layer appeared uniform, rich in mollusc fragments and polleniferous. The absence of other mineral inwash suggests that this is not a fluvial feature. However, a circumstance can perhaps be visualised in which there was a flash flood in the valley which led to bank overtopping by the Gypsey Race. The floodwaters carried pebbles onto the flood-plain of the Gypsey Race, but the finer material was kept in suspension as the flood surge washed back to the stream, leaving no trace of the finer sediment load on the flood-plain. This must be considered somewhat unlikely because the deposition of the chalk would appear to have been a single event. In that case why should such a flood occur only once? Other lesser floods would have been expected in which smaller gravels and sands were deposited. Furthermore, the bed of the Gypsey Race is now made up of material washed from the till sheets. Had the floodwaters picked up pebbles from the bed of the Gypsey Race there would not have been such a high proportion of chalk amongst the pebbles deposited on the flood-plain.

The presence of mollusc testa in a good state of preservation in the horizons above and below the chalk layer suggests that this most particular distribution is not the product of acid solution of the chalk in other layers.

Earthworm activity should not be discounted as the presence of worm egg capsules down to, but not beyond, the chalk pebble layer indicates that there was some earthworm activity in these levels. When a large Populus alba fell due to wind-blow, it was noticed that the layer of chalk fragments was immediately below the plate-like root mass of the tree. This suggests that the chalk fragments coincide with the layer of permanent waterlogging in the soil.

The pollen record within this zone showed a degree of zonation, although the samples between 4 and 34 cm were not separated by POLZON or TWINSPAN. If the soil was regularly disturbed by earthworms the redeposition of pollen can be expected to result in a homogenised pollen record even though the larger fossils still show a degree of zonation (Dimbleby, 1962). That pollen can pass through the gut of many soil organisms was demonstrated by Faegri (1971); the exine is left undamaged and so considerable biological reworking of pollen is possible without any selective preservation becoming apparent.

A difference between the samples, which neither of the statistical techniques would detect given the restricted data sets which were used, was the change in species diversity. In an homogenised soil there would be little or no species diversity between samples, apart from the effects of selective preservation. The apparent drop in species diversity at 22 cm (Fig. 8.1) does not appear to be a product of selective preservation as those species indicative of such conditions, e.g. Pinus, Tilia and Polypodium, did not increase in that level. This might suggest that even if earthworms were present in the soil, the mixing of soils is not advanced and that the pollen evidence, whilst treated with caution, should not be disregarded.

A further possibility is that the chalk fragments are the product of a plough horizon. The presence of pot and bone in the chalk pebble layer could support an hypothesis involving the active participation of man in the formation of this feature. The pot sherds were provisionally identified as belonging to the Saxon period by Dr J. Dent, the County Archaeologist for Humberside. This date corresponds well with the inferred radiocarbon date for this level of c. 1200 B.P.. The chalk must have been brought onto the site and it may be that the chalk fragments represent an attempt to marl the site. The scatter of chalk is so loose, however, and the fragments so coarse, that a marling horizon was thought an unlikely explanation by Dr J. Dent who visited the site in 1985. These criticisms aside, if the fragments do represent a plough horizon it was a short-lived attempt at agriculture, as it was not revealed in the macrofossil samples. The depth of disturbance caused by saxon ploughs was very shallow and subsequent compaction might have resulted in it being too fine a feature to have been recorded by the 4 cm sampling depth used for the macrofossil study.

Dr J. Dent also expressed doubts as to whether the scatter of chalk represented a trackway and could not offer an anthropogenic explanation for this layer. Professor D. Walker was also shown the sediment profiles and he was unable to suggest a natural mechanism whereby this band of fragments could have accumulated.

The cause of the horizon of chalk fragments is not apparent beyond concluding that they are probably an anthropogenic feature. The most important conclusion that may be drawn is that whatever caused the deposition of the chalk layer does not seem to have disrupted the environmental record in this deposit. An investigation of the biological data may indicate what the activity of man was, even if it does not directly explain this stratum.

Biozone WGP-8

Vegetation

Throughout this biozone there was a progressive change in the bryophyte flora from that of a fen community towards that of open woodland. The bryophytes at 36 to 32 cm were of a fen association, one which had been consistently present since the first peat formation, *Calliergon cuspidatum*, *Scorpidium scorpioides* and *Amblystegium riparium*. At 28 to 24 cm the moss flora was characteristic of a wet woodland with the species: *Aulocomnium androgynum*, *Eurynchium* cf. *praelongum* and *E. schleicheri*. *E. praelongum* was one of the species mentioned by Clapham (1940) as being characteristic of dry fen in shaded locations. Another species mentioned in the same section (Clapham, 1940) was *Lophocolea bidentata*. This species was found in the sample at 8 - 4 cm, an unusual find as liverworts are seldom recorded as fossils. The pollen record will only be dealt with briefly for fear of over-interpreting what may be a reworked horizon. It is evident from the diagram that Cyperaceae reached a peak at 22 cm and then declined throughout the remainder of this zone. Aquatic taxa were virtually absent from these levels. The taxa which increased were: Salix, Pinus, Liguliflorae and Centaurea nigra. The increase in Salix was most noticeable in the preliminary diagram where it increased from a steady 2% in the previous biozone to a consistent 8% in the levels above 30cm. Godwin (1975) observed that Salix seldom exceeded 10% of the pollen total; this was supported by the result of the modern analogue study where only 5.8% Salix pollen was yielded by a trap set within a small Salix copse. From Fig. 7.3 it may be seen that Salix attained a maximum of 4% of the dry land pollen sum.

The rise and fall of Cyperaceae might be explained by the contraction of an open area of water providing a larger, or closer area, suitable for the growth of Cyperaceae. The subsequent decline of this taxon, from 40% to 8% of the dry land pollen, might be caused by the shading of the site as the drier land is invaded by Salix. Alnus pollen does not change in frequency, although there is a peak of Alnus fruits in the upper 12cm. The colonisation and shading of a fen was recorded in an Oxfordshire fen by Clapham (1940). In that study Carex paniculata tussock formation was observed to have taken place during the first stage of drying. This was halted by the arrival of carr species and there followed the death of the tussocks due to shading by alder woodland.

Also represented in the pollen rain in biozone WGP-8 were grasslands, characterised by the presence of Sanguisorba minor and Helianthemum. Cerealia pollen and a wide range of arable weed species provided evidence of the practice of arable cultivation at this time. The greatest proportion of large sized (>44 µm) Gramineae occurred at 34 to 28 cm, suggesting that arable farming was at a peak at this time. This would have been c. 1100 B.P..

The mollusc record indicated a maximum diversity of 19 species at 16 to 12 cm. In the lowest sample in this zone 14 species were recorded; all were hygrophilous and 10 species were aquatic or semi-aquatic. The obligate hygrophiles accounted for 91% of the total. The commonest taxon was the marshland dweller Succinea putris (18%), which can survive in stagnant conditions. Other slum-dwellers from this level were: Anisus leucostoma, Pisidium personatum and Bathyomphalus contortus. These species though primarily part of an aquatic fauna will live in almost any moist muddy environment. Standing water is indicated by the presence of Pisidium nitidum, Planorbis laevis and Valvata piscinalis. In each level the proportion of aquatic taxa decreased and the range of dry land taxa diversified. At 24 to 20 cm the aquatic and waterside taxa were reduced to 59% and half the species total was of dry land taxa. The waterside taxa never totally disappeared because the site always remained a wetland, but the obligate aquatics were reduced to <2% at 12 to 8 cm and the hygrophilous dry land mollusc Carychium minimum dominated the assemblage with 63% of the total count. The abundance of C. minimum, Aegopinella nitidula, Vitrea crystallina and Euconulus fulvus, in the levels between 24 and 0 cm, suggests a damp shaded environment. The molluscan evidence suggests a drying and progressive shading of the site which is entirely in accord with the bryophyte and pollen data. This trend is reflected in the DECORANA ordination of the mollusc data (Fig. 7.21) in which there is a clear trend out of the wetland towards the woodland sites.

The greatest detail of this change in the vegetation comes from the propagule record. It can be seen from Fig. 7.7 that there was a peak of aquatic taxa indicated at 40 cm. By 32 cm the peak had dropped dramatically, as had the curve for the fenland species. At the same time there was an increase in *Stellaria media* (these data are absolute and so the rise and fall of species are not mathematically related) and of plants of disturbed ground such as *Chenopodium album*, *Atriplex*, *Polygonum* spp. and *Urtica urens*. This would seem to indicate a drying of the fen and the presence of disturbed ground. It is a curious feature of these diagrams that despite this peak of *Stellaria media* the distinctive pollen of this species was not recorded. The ecological conditions of the fen continued to change, *Stellaria media* declined in abundance, as did the taxa of disturbed ground, and ruderal taxa. However, *Urtica dioica* increased throughout this zone. Such a progression might suggest the bare ground becoming overgrown and increasingly shaded by *Salix* and *Alnus*. The increase in *Urtica dioica* may indicate an increase in the phosphate content of the soil. Contemporaneous with the rise of *U. dioica* the fenland taxa are shown to increase. Whereas the previous peak had been attributable to *Menyanthes trifoliata* this one was caused by a flush of *Scrophularia* at 16 cm. This is a genus containing plants which generally favour damp shaded environments. *Silene dioica* was abundant at 12 cm and this is a plant which favours well drained woodland conditions where the soils are rich in nitrates (Clapham *et al.*, 1962). The loss of the heliophilous species *Valeriana officinalis*, *Valerianella dentata* and *Lycopus europaeus* is evident in the samples higher than 16 cm. The local herb flora lost much of its diversity, but still contained *Ranunculus* sec *Ranunculus*, *Juncus conglomeratus* agg., *Cirsium* and *Lychnis flos-cuculi*. *Rumex*, *Aphanes arvensis* and *Euphorbia exigua* are weeds of arable ground and these, like the weeds of disturbance, could indicate soil disturbance on the site, or the close proximity of agricultural land.

The evidence seems clear that the fen was progressively drying out and that trees encroached onto the previously wet area, shading out the heliophilous species.

To return to the discussion regarding the level of chalk fragments, it is apparent that man was active in the local environment, which does not conflict with the suggestion that the chalk pebble layer was an anthropogenic feature. To carry chalk fragments onto a fen and scatter them over the surface required a considerable investment of time and effort. It was presumably for some purpose.

The drying of the fen may have been initiated by the onset of the 'Little Optimum' at *c.* 1200 B.P. (Goudie, 1977); the mild winters and dry summers may have been sufficient to bring about the observed change. However, whatever caused the change was not sufficient to reduce the flooding by the Gypsey Race as the sedimentation does not appear to have changed throughout this period. It is possible that the climatic improvement led to increased evaporation rates so that the standing pools of water were present for less time each year and this encouraged the local inhabitants to try to drain the fen. This would have needed the cutting of drainage ditches. In so doing there would be considerable soil disturbance and the bare ground would be colonised by weed species such as those listed above. This could help to explain the sudden increase in the weeds of disturbed ground.

It seems unlikely that there was such a shortage of land for arable farming that the draining of a wetland should be attempted. This would have represented an enormous investment of time and energy for the reclamation of a relatively small area of land. Perhaps the land was wanted because it was wet.

There are relatively few uses for a wetland but they include the cultivation of water-cress and osier beds. It should be remembered that the two are not mutually exclusive. Few seeds of Nasturtium aquaticum were found and it would be hard to reconcile the increasingly shaded nature of the site with cress cultivation. It is assumed that this was not the main use of the fen.

The palaeoecological data suggest an increasingly shaded site and yet there was little change in the pollen curves of the arboreal taxa other than for Pinus and Salix. Pinus rose in the uppermost levels but this might be attributable to selective preservation, planting, or a regionally derived component. It is unlikely that it would ever have grown on the fen surface. The shading tree is therefore most likely to have been Salix. This would support the argument that the fen was being used as an osier bed.

An osier bed would seem highly probable, as it would explain most of the characteristics of this data set and the name of the site. The site is listed by the Nature Conservancy Council as an ancient osier (Salix viminalis) bed (Dr C. Raphe pers. comm.). The site is also the only known location of Salix purpurea in East Yorkshire (Dr D. Boatman pers. comm.). A disjunct distribution such as this is usually taken as being a sign of the antiquity of the habitat. S. purpurea was a species commonly grown with S. viminalis in osier beds as it is another of the willows with very pliable stems. The wands were cut every three to four years for use in basket-work, making hurdles and for string (Godwin, 1975). Although the coppiced stems grew rapidly it may be expected that they would bear little pollen and fruit. Whereas with the creation of most woodlands there would be a degree of soil disturbance from planting, this would not be expected in an osier bed as cuttings are simply pushed into the wet ground.

An osier bed is still in evidence in the central, wettest strip of Willow Garth, although the osiers have been succeeded by taller species close to the sampling site.

It is likely that, in a region where the sites for growing osiers were so rare, the osier beds were highly prized. This might explain why during later land shortages no attempt was made to drain and plough the Willow Garth.

The riddle of the chalk fragments has still not been solved and no testable hypothesis can be presented to explain their presence. There is no evidence to suggest that the chalk was laid as paths and has since spread, although a full archaeological investigation of the site might reveal such a pattern. If the soil disturbance early in this biozone was due to the cutting of drainage ditches the purpose of these was presumably to remove the surface water, rather than attempt to drain the fen itself. This would only have needed shallow channels which may have become full of silt and are no longer visible. Alternatively, the present drainage ditch which runs west to east through the reserve might be an ancient channel which has been renewed in modern times.

It is perhaps appropriate briefly to consider another mediaeval site, that of Wharram Percy, a village high on the north-western portion of the Yorkshire Wolds. It lies in a steep sided valley which formed one of the head waters of the ancient river system which once drained into the Great Wold Valley. Wharram Percy was occupied from early Saxon times until the enclosures of the fifteenth century, and has provided the most complete excavation record of a deserted mediaeval village in Britain (Hurst, 1979).

The samples for pollen analysis were taken from organic lenses in sediment which had accreted behind the dam of the village pond. The samples do not represent one continuum but three periods of sedimentation (Appendix 2). The upper and lower periods of accumulation are characterised by high, as much as 93%, Liguliflorae pollen, but as these levels are also of very low pollen concentration, _c._ 30000 grains g^{-1} this is likely to be the product of selective preservation. Liguliflorae pollen has been shown by Havinga (1971) to be highly resistant to corrosion. The middle period of deposition, however, reveals a mixed assemblage of fenland plants, e.g. Caltha and Lychnis, the arable plants, Cerealia and Polygonum spp. and grassland components, e.g. Sanguisorba minor and Helianthemum. This is an essentially similar mixture of habitats to that seen in the diagram from Willow Garth from this time. The woodland component in the pollen input at Wharram Percy was less than 10%, and it is noticeable that despite the presence of selective preservation Tilia was totally absent from this record.

Overall, this record represents an essentially open habitat in which there is evidence of a mixed agricultural economy in which only isolated patches of woodland, or indeed only isolated trees remained. This pattern repeats the trends shown at Willow Garth.

Biozone WGP-8

Climate

The climatic influence on the environment in this biozone has been obscured by the actions of man although the return of Sanguisorba officinalis may indicate a climatic amelioration which would be consistent with the concept of the climatic optimum in Saxon and early mediaeval times. This increase in temperatures may have initiated the drying of the fen at Willow Garth, implying that there was no corresponding increase in rainfall.

8.8 The Chalk Grasslands

The view that the chalk grasslands have an anthropogenic origin and date to the neolithic introduction of sheepwalks was put forward by Tansley (1939). Previously it had been assumed that the chalk grassland was a natural community which had survived throughout the post-glacial period. The school of thought that the grasslands could not have survived the forest expansion of the Boreal and the Atlantic period was reinforced by experiments in which grazing animals were excluded from grasslands. Scrub species, e.g. Crataegus monogyna and Cornus sanguinea, were found to colonise quickly (Wells, 1969). These were thought to be the pioneers of forest cover. Similar results were observed after the myxamatosis epidemic of the 1950's had virtually eradicated rabbits from the chalklands of Britain (Thomas, 1960, 1963). This was seen as evidence that the survival of the chalk grasslands was dependent on disturbance initiated by man. Neolithic settlers were believed to have been the first to shape the environment. Consequently, the origin of the downland as an open landscape was thought to date from the neolithic period.

As the role of mesolithic man in shaping the landscape becomes more apparent this simplistic view may need to be revised. Certainly many of the mollusc assemblages from the southern chalklands show a transition from a wooded environment to one of a grassland, e.g. Avebury (Evans, 1972). Even at this site Evans described the woodland as having been 'light'. It is not possible, from the mollusc data alone, to determine whether this was a continuous canopy producing light shade, or whether it was a parkland landscape of copses separated by grassland. The Avebury site never lost the open ground indicator species such as Vallonia excentrica, a taxon which requires dry open grassland. Other diagrams, e.g. Horslip, suggest open ground conditions prevailing before a forest 'recolonisation' (Evans, 1972). On what grounds can the authors state that this is recolonisation as opposed to colonisation ?

It would be illogical, in view of the existing evidence, to suggest that the chalklands were completely open. Certainly there existed a forest cover, as suggested by the molluscan and palynological evidence, but the degree to which a complete forest closure took place is much harder to estimate. As stated previously, the greatest difficulty is to find chalkland sites yielding a sufficiently wide range of fossil types to provide a detailed palaeoecological record. Molluscan evidence is valuable, especially when there is so little palynological evidence available. However, the limitation of no host-plant-specificity and the effects of microclimate make the interpretation of these data rather vague and subject to strong local bias.

Only a few taxa with distinctive palynomorphs such as Helianthemum, Sanguisorba minor, Centaurea scabiosa and Gentianella are specifically calcicolous. The pollen of many grassland plants is often morphologically inseparable from that of plants of other habitats. Many of the species strongly characteristic of the chalk grasslands are in the Cyperaceae or the Gramineae. The pollen of species in these families is not readily distinguishable and so is of limited use in identifying specific habitats. Additionally many grassland plants are entomophilous, e.g. Linum catharticum, and so their pollen is under-represented in fossil spectra. Similarly, the high species diversity of chalk grassland means that each species is comparatively rare, further reducing the chance of finding pollen from one of the recognisable calcicoles.

A narrow woodland screen between the deposit and the grassland will intercept much of the pollen and may well smother the pollen of the grassland taxa with that of arboreal taxa. This was a problem identified by Oldfield (1970). Even so, some palynologists still sought to generalise about the chalkands, though their sites were some distance from the chalk outcrop (e.g. Thorley, 1981). Of the sites studied by Waton (1982), only one, Winchester, may be realistically expected to reflect the vegetation of the local downland. At Winchester Sanguisorba minor was recorded from a deposit prior to the dated level of 5630 ±90 B.P. (HAR-4342). This could suggest the presence of chalk grassland, a point which Waton did not discuss. Such reticence is understandable, as to lay emphasis on such slender evidence would be to over-interpret the data. However, so long as only one line of palaeoecological evidence is considered, this may be as much evidence of 'early' chalk grassland as could be expected.

The suggestion that forest closure was not complete is not novel; Pigott and Walters (1954) proposed that the downlands were of relatively open aspect and that chalk grassland refugia existed throughout the post-glacial period. It was suggested that these were natural areas on steep slopes where the soil was too thin to support the growth of trees. This hypothesis remains to be tested.

The evidence from the present study indicates that the Pre-Boreal forest never formed a closed canopy as *Helianthemum*, *Plantago* spp., *Centaurea nigra* and *Campanula* were all present during this period. The Gramineae pollen percentage remained high and, as suggested by the statistical analysis of Gramineae pollen sizes, much of this pollen was regionally derived.

It is suggested that there had been considerable forest disturbance before the canopy of the Boreal forest closed, resulting in open areas in which the above grassland species persisted. The *Betula* peak at *c.* 8200 B.P. was brief and the massive pollen production of this tree may have obscured the lower production of a grassland element. After this peak *Teucrium botrys*, *Bellis* and *Plantago media/major* were recorded, plus other taxa which could have been components of a grassland flora: *Hypericum*, Liguliflorae, *Bidens* type, *Achillea* type, *Veronica*, *Galium*, *Vicia* type, and the fruits of *Ranunculus* sec *Ranunculus*, *Potentilla erecta* and *P. reptans*. Even if this latter category of plants was all derived from the fen the Gramineae, which were present at up to 16% of dry land pollen, and the herbs such as *Teucrium botrys* indicate the presence of dry grassland. The continuing presence of the chafer, *Philopertha horticola*, throughout the *Betula* dominated levels would support the proposal that grasslands persisted during this period.

Between *c.* 8000 B.P. and 4000 B.P. there was no record of the vegetational succession from this site. Evidence for the mesolithic occupation in this part of the Wolds comes from the three sites of Kilham, Burton Fleming and Bessingby. The Bessingby and Burton Fleming sites are thought to have been mid-late mesolithic. Once mesolithic man had started to clear the forests it is likely that the benefits to the hunter-gatherer would have been realised and the practice continued. The traditional view of neolithic peoples introducing domesticated livestock for the first time has been challenged by Jarman (1976), Roux and Leroi-Gourhan (1965) and Whittle (1980a,b). They suggested that the domestication of animals may have been a gradual progression starting with reindeer, wolves, red deer and wild cattle. Pigs were a gradual introduction and the expansion to include sheep and goats was a final, not an initial, stage in the process. The mesolithic settlers were probably exploiting some or all of these animals and in doing so were providing grazing areas for them.

The pollen record from the buried soil at Kilham suggested an open landscape in which two phases of agriculture, separated by a period when the land lay fallow, took place prior to 4800 B.P. (Dimbleby and Evans, 1976).

The hypothesis that the neolithic peoples may have chosen the Wolds to settle because of a relatively open landscape may well be true, not as a result of trees failing to colonise the chalklands, but as a result of continual anthropogenic disturbance.

The ecological implications of this are highly significant, for if the chalk grasslands survived in local patches throughout the post-glacial period then they must be considered as one of the oldest British plant communities. They may even have survived in some form on glacial forelands, such as the Wolds, throughout the Devensian period.

The extent of these mid-post-glacial grasslands cannot be estimated from the analysis of a single site, but the necessity for futher work on the British chalklands is reinforced by these results which depict a history of useage totally different from those shown to date.

CHAPTER 9: CONCLUSIONS

9.1 GENERAL CONCLUSIONS

The palaeoecology of the British chalklands has been a matter of academic speculation, with very little data from Quaternary deposits to determine a conclusion to the debate. This has been the consequence of a paucity of sites where there are suitable conditions for the preservation of organic material. Those deposits which have been found were mainly located in the south-east of England and results from these have been taken to indicate an environmental history for all the British chalklands.

That the Yorkshire Wolds lie some 340 km north of the southern chalklands means that other ecological factors may have affected the rates of species immigration. Factors which might differ between the northern and southern chalks would include: distance from the European landmass, temperature, rainfall, late-frosts, the duration of snow-lie, and day length. Indeed the ecological range of some species may be reached at a point between the two chalkland regions; cases in point would be Teucrium botrys, cut-leaved germander, or Lysandra coridon, the chalkhill blue butterfly. Both are species which occur on the southern downs but which are absent from the northern Wolds.

There is also no guarantee that the pattern of colonisation by man would have been the same, nor that the colonising cultures practised the same technologies.

The shortage of sites for palaeoecological study on the Yorkshire Wolds was no less acute than in the south of the country, and of the sites investigated only one was found to yield a late- and post-glacial pollen sequence. Rather than dissipate the resources available for this study on an additional range of peripheral sites of questionable relevance, it was decided to carry out an in-depth study of this one location. It was hoped that through the analysis of different palaeoecological indicators a far more complete understanding of the processes affecting the site could be achieved than if the pollen alone was analysed.

In order to provide a framework from which deductions regarding environmental change could be made a series of modern analogue studies was undertaken. This involved quantitative studies of pollen, plant macrofossils and molluscs from sites where a detailed vegetation survey had been carried out.

Data obtained from these studies were treated statistically to obtain pollen weightings (R-rel) for the commonest arboreal taxa. The percentage data used with this technique by Bradshaw (1981a) were replaced with absolute values and the use of 'girth at breast height' was found to be a less significant indicator of pollen production than the measure of 'weighted canopy area' adopted in this study.

TWINSPAN and DECORANA, multivariate analysis programs devised by Hill (1979a,b), were used to analyse the modern analogue data and these results in turn were applied to the analysis of the fossil pollen, propagule and mollusc data. The modern pollen rain was found to reflect accurately the regional environment. Betula was a consistent overproducer in woodlands and Gramineae were considered to have been overproducers in almost all locations. There seemed to be very little correlation between the Gramineae pollen yield and the number of occurrences of Gramineae in a sample area. This was attributed to the predominantly open aspect of today's landscape. Even in woodlands as much as 20% of the pollen was derived from a regional Gramineae input. Tilia was found to be a heavy pollen producer within the stand but the proportion of Tilia pollen fell rapidly outside of that area.

A closer representation of the species occurring within 5 m was obtained by plant propagules than by pollen, particularly in open habitats. In closed woodland habitats there was less air movement and hence less chance of seed dispersal. Seed concentration and diversity was much reduced in these sites; woodland species in general seemed to produce far fewer seeds. The exception to this was Betula. Whereas most propagules were likely to have been derived from within 5 m of the sample site Betula propagules were recorded more than 100 m from the nearest source and the over-representation within 20 m was such that Betula occurring as a scarce woodland tree would dominate the seed and fruit assemblage with more than 90% of the propagule sum.

Lamb (1984) analysed the pollen content of surface samples and moss polsters from Labrador and then used this as a framework on which to superimpose the fossil pollen values. These were used to define the changes in fossil pollen records from the tundra region of Labrador (Lamb, 1984, 1985). In the present study this technique was extended to incorporate statistically defined vegetation types from which the data were gathered. This was used in preference to the semi-quantitative data obtained from forestry reports which Lamb used to define the vegetation types. The statistical techniques DECORANA and TWINSPAN were applied rather than Principal Components Analysis (the latter had been used by Lamb) due to the 'arch-effect' which is a common fault of a Principal Components Analysis (Gauch, 1982).

The constrained classification program POLZON was utilised to zone the fossil data sets and, although unconstrained, TWINSPAN produced a very similar classification for both the pollen and plant propagules data sets. This may be seen as evidence of the ability of TWINSPAN to handle large, complex data sets of this kind. The use of DECORANA and TWINSPAN was to an extent experimental, as, at the time of writing, this is believed to be the first application of these programs to palynological data. The results obtained through these analyses were interpretable and entirely ecologically consistent between data sets.

The comparison of the timing of key changes in the local (macrofossil) flora and the extra-local and regional (pollen) flora was used to determine whether the Gramineae pollen size distributions varied in phase with the local or the regional vegetation changes. The result of this experiment was that the Gramineae size distribution zones, as defined by POLZON, and the ecological distance inferred between them, fitted very closely to the regional vegetation changes. It was therefore concluded that the majority of Gramineae pollen was regionally, or extra-locally, derived and that fluctuations were consequent on regional rather than local vegetation changes.

The late-glacial vegetation of the Yorkshire Wolds was an open *Betula* and *Salix* scrub forest, with a rich herb and wetland flora existing in the Windermere Interstadial. With the characteristic climatic deterioration which led to zone III, or the Loch Lomond Readvance, *Betula* was much reduced. Timber of *Alnus* was present in these deposits which might suggest that the Great Wold Valley may have had at least local stands of *Alnus* throughout the late-glacial period. At 9460 ±80 B.P. peat growth started at Willow Garth, a period represented by the pollen and propagules of a rich tundra flora.

With the onset of climatic amelioration a *Betula* forest developed, but the grassland taxa were still present even at the end of this pre-Boreal period when *Pinus* pollen started to increase in abundance. At *c*. 9200 B.P. this progression appears to have been halted by forest disturbance. The return of *Betula* during the succeeding period, a time of further climatic improvement, was interpreted as the growth of *Betula* as a secondary forest taxon. Insect evidence, fruits and other macrofossils indicated the presence of a temperate forest flora such as would have been expected in the Boreal period. These forest trees failed to dominate *Betula*; also weeds of disturbed ground and grassland species were recorded throughout this period. It was suggested that mesolithic man, of which there are abundant remains in the Great Wold Valley, was managing the forests to improve the grazing potential of the valley. The resultant open glades provided the habitat in which chalk grassland species could survive. The local cessation of management appeared to take place at *c.* 8200 B.P. and there was then a period of rapid forest change as the plagio-climax vegetation was ousted by the temperate forest trees. Whether man continued to disturb the forest at other sites along the Great Wold Valley at this time is uncertain, but the finds of flints from the later stages of the mesolithic period at Bessingby, Kilham and Bishop Fleming, suggest that this might well have been the case.

The beginning of the climatic optimum was recorded at *c.* 8200 B.P. with species such as *Teucrium botrys* indicating a slightly warmer climate than that of the Wolds at present.

A standstill level in the core between *c.* 8000 B.P. and 4000 B.P. did not allow any conclusions to be drawn on the local probability of an elm-decline. When deposition recommenced there was evidence of cereal cultivation, open grassland and mixed deciduous forest in the locality. It was suggested that the neolithic settlers may have moved into a landscape already fashioned by man in which there were extensive clearings and belts of secondary woodland. *Tilia* may have been an important forest tree at this time but caution was urged when attempting to establish the abundance of a taxon known for the durability of its pollen.

The Yorkshire Wolds would, most likely, have been wooded during the Boreal and Atlantic periods with *Quercus* as an important forest component. *Tilia* may have been important, but insufficient unequivocal evidence has been gathered to allow firm conclusions to be drawn. The extent of forestation is open to question and it is likely that once man had learnt to manage the forest to increase the carrying capacity of game he would not have forsaken this practice. The duration of the clearances would appear to have been in excess of 100 years, during which time grazing animals prevented seedling regeneration. This may have been widespread and only further work on the palaeoecology of the Wolds will determine this.

There was evidence to indicate that Bronze Age land use included both cereal cultivation and permanent pastures. Clearance had reduced the arboreal pollen input to < 20% of the dry land pollen sum.

Throughout the mid-Flandrian the fen flora at Willow Garth had been steadily diversifying but this trend was reversed in the Saxon period. The apparent drying out of the fen co-incided with the occurrence in the stratigraphy of an unexplained layer of chalk fragments. These may represent a brief attempt to bring the fen under the plough, but whatever caused this feature did not materially affect the quality of the palaeoecological record of the subsequent sediments. Sedimentation at the site continued and it was suggested that the land use at Willow Garth changed to that of an osier bed at c. 1200 B.P..

Only by analysing different types of fossil did the picture presented emerge. If the pollen alone had been analysed then the interference by man in the mesolithic forests might well have gone unrecorded. This study provides an example of how the different disciplines, when used together, yield an image greater than the sum of the individual parts.

9.2 R-REL VERSUS MULTIVARIATE ANALYSIS TECHNIQUES

The use of R-rel values and of multivariate analysis techniques produces two different sets of answers. The utility of those answers depends entirely on the question that the researcher is posing. The restriction of the R-rel method is that it relies on the direct comparison of vegetation and pollen data, whereas the other method relies on the comparison of two sets of pollen data and only a broad vegetation description. This offers a much more rugged framework for comparison and few constraints on its implementation.

If the constraints of the R-rel model are met, and in this instance they were not, then this is the most accurate method of woodland habitat reconstruction. However, the criteria are so demanding and inflexible that the widespread use of this model is greatly reduced. The use of modern analogue sites in multivariate analysis, in combination with programs as robust as TWINSPAN and DECORANA, offers a wide range of comparisons which can be made at whatever level of exactness the researcher requires.

In the course of this study it has become apparent that bank-overtopping was probably an important environmental component, and yet this is a completely unknown quantity in terms of its pollen yield. If analogue studies are to be used in the future further refinements to the methods of pollen trapping, in all types of habitat, are required, especially to take account of pollen carried in the surface water during times of heavy rain or flooding.

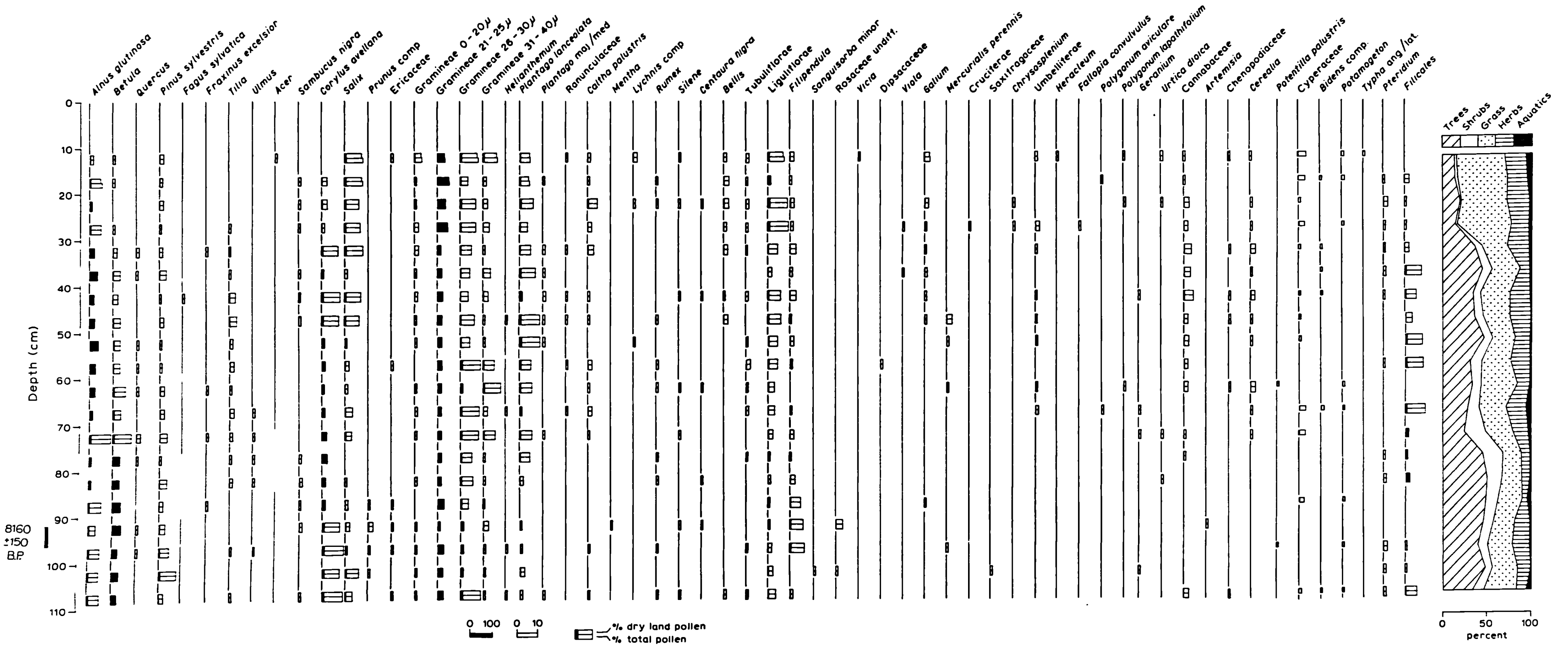
9.3 FUTURE STUDIES

Willow Garth has been designated a site of Special Scientific Interest on the strength of these findings. This may safeguard the future of this site, but if any other sites exist, which it should be made clear we failed to find despite an extensive search, they should be sampled quickly, as in the present economic climate marginal wetlands are being ploughed out at an unprecedented rate.

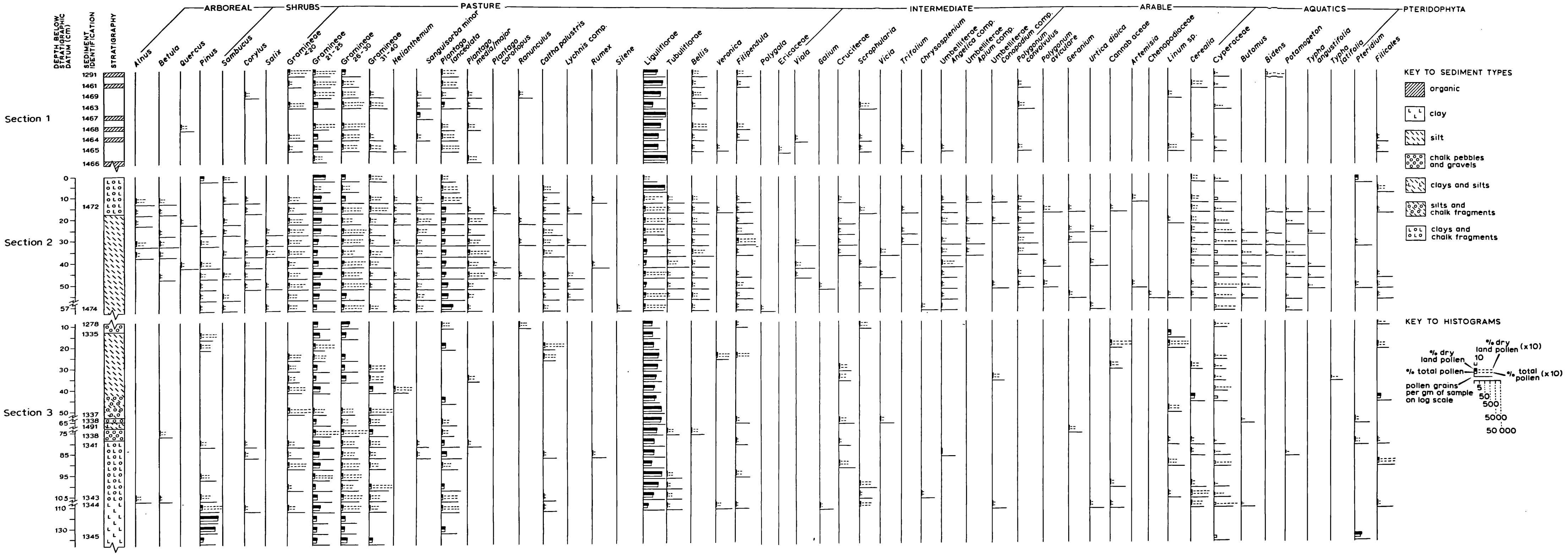
The most obvious follow-up work to this project would be for archaeologists to recommence their searches for mesolithic sites on the Yorkshire Wolds, and as an immediate starting point to carry out field-walking in the Great Wold Valley, especially on the sandy deposits adjacent to Willow Garth.

Dr H. Kenward suggested that a larger volume of sediment should be used for a further insect analysis. The insects were well preserved but the 0.5 - 1 litre samples used in this survey were not sufficient for a quantitative analysis to be undertaken.

It would seem worthwhile for future studies of the all too rare deposits on the chalk to undertake as comprehensive an analysis as possible, to include molluscs, plant propagules, insects, bryophytes, timber and close radiocarbon dating in addition to the standard palynological investigations. An immediate starting point would be the site at Winchester which may yield a wealth of further information if treated in this way.



APPENDIX 1 PRELIMINARY POLLEN DIAGRAM FROM WILLOW GARTH



APPENDIX 2 POLLEN DIAGRAM FROM WHARRAM PERCY

APPENDIX 3: LIST OF FOSSIL INSECTS RECOVERED FROM WILLOW GARTH

PENTATOMOIDEA

Elasmucha grisea L.

LYGAEIDAE

Cymus sp.

GERRIDAE

Gerris sp.

CARABIDAE

Agonum sp.

Amara sp.

Bembidion sp.

Calathus sp.

Phyllochthus cf. lunulatum

Pterostichus cf. diligens

DYTISCIDAE

Colymbetes fuscus L.

Colembytinae (undiff.)

Dytiscus sp.

Rantus sp.

GYRINIDAE

Gyrinus sp.

Hydroporinae (2 spp.)

HYDROPHILIDAE

Chaetarthria seminulum Hbst.

Coelostoma orbiculare F.

Helophorus sp.

Hydraena sp.

Hydrobius fuscipes L.

Limnebius sp.

Ochthebius sp.

STAPHYLINIDAE

Acidota sp.

Geodromicus sp.

Metopsia retusa Steph.

Staphylinus sp.

Tachinus sp.

CANTHARIDAE

Cantharis rustica Fn.

HELODIDAE

Cyphon sp.

DRYOPIDAE

Dryops sp.

SCARABAEIDAE

Aphodius (*Heptolaucus*) sp.

Geotrupes sp.

Phyllopertha horticola L.

Serica brunea L.

CHRYSOMELIDAE

Donacia sp.

Donaciinae (undiff.)

CIRCULIONIDAE

Apion sp.

Bagous sp.

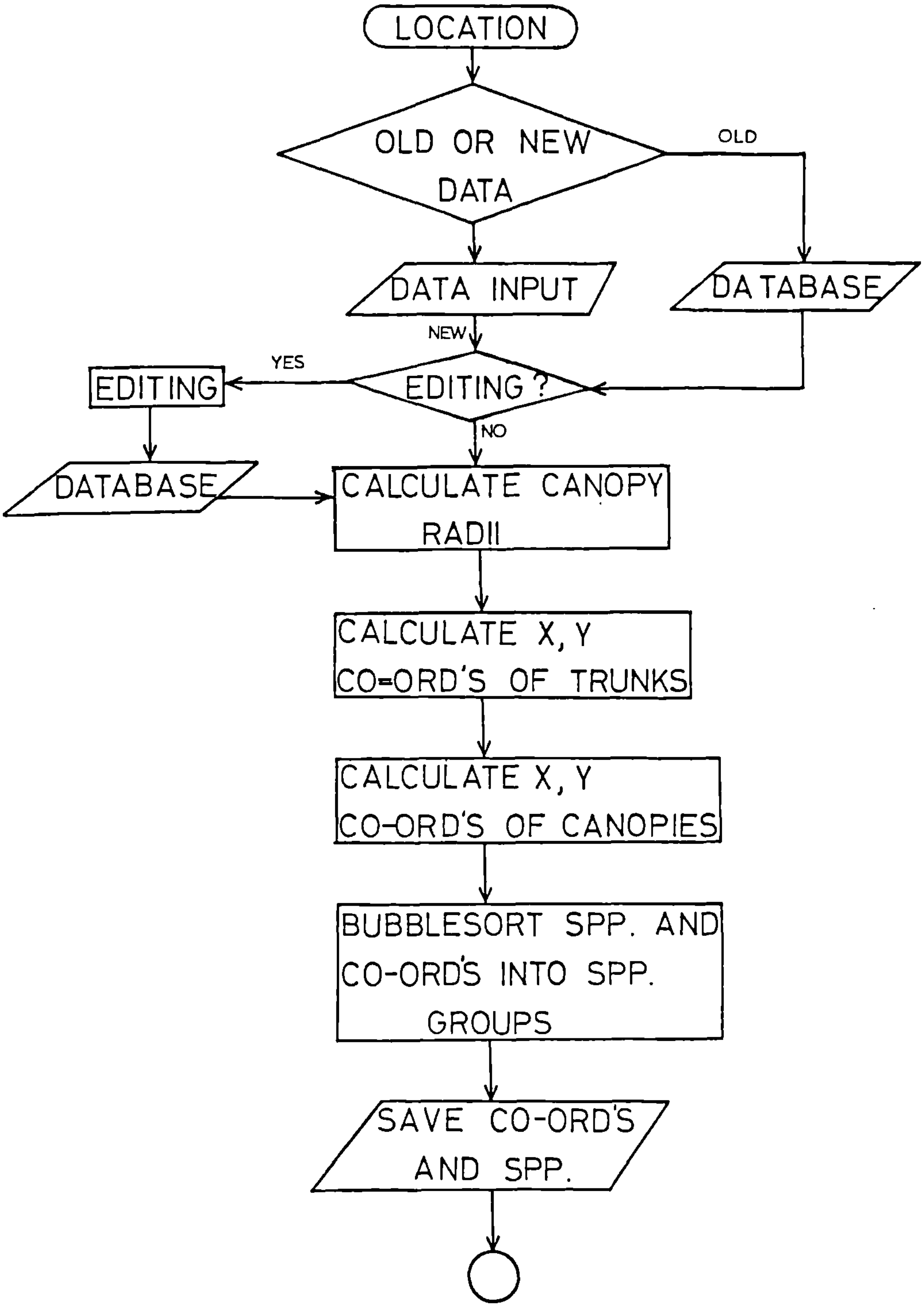
Baris sp.

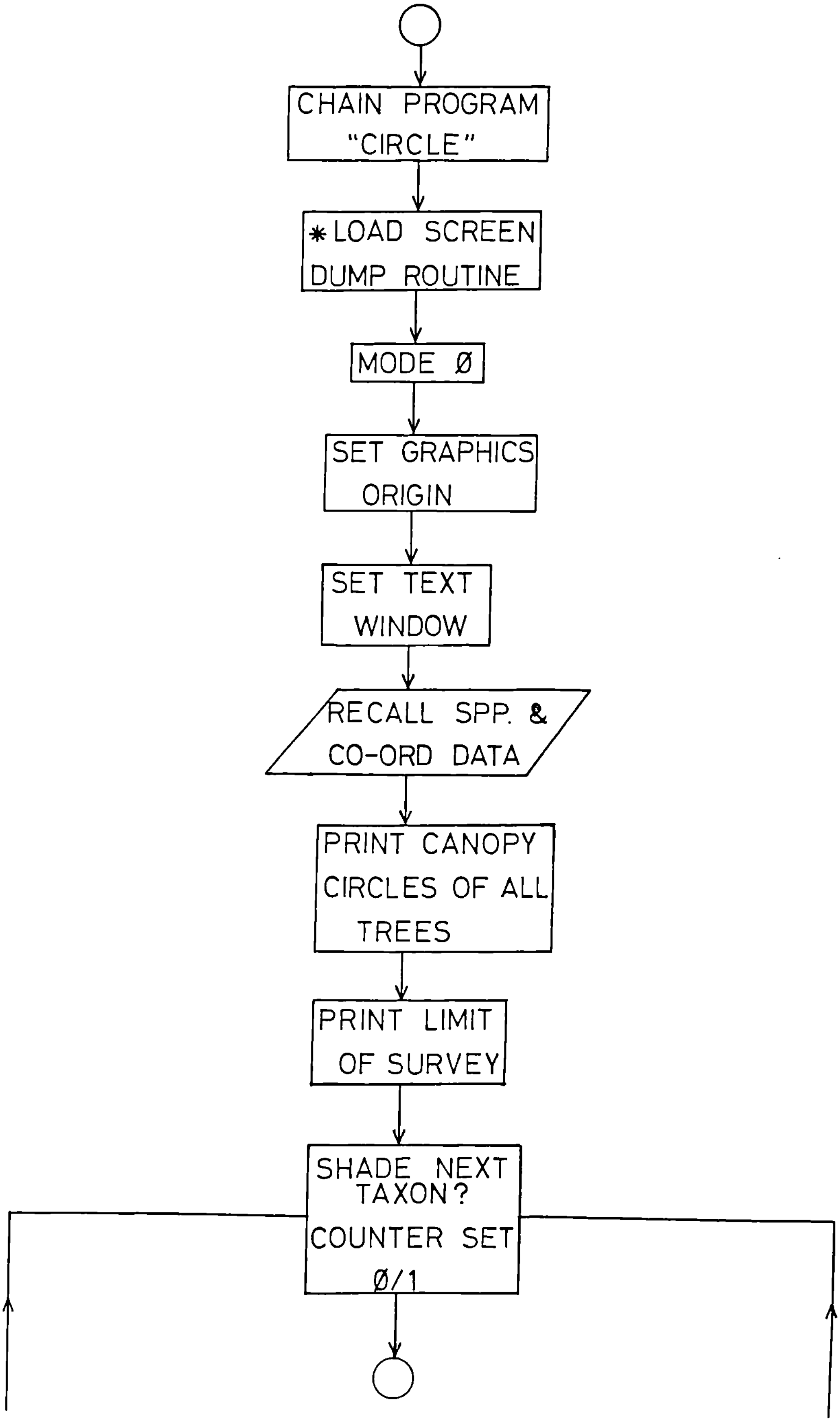
Notaris acridulus L.

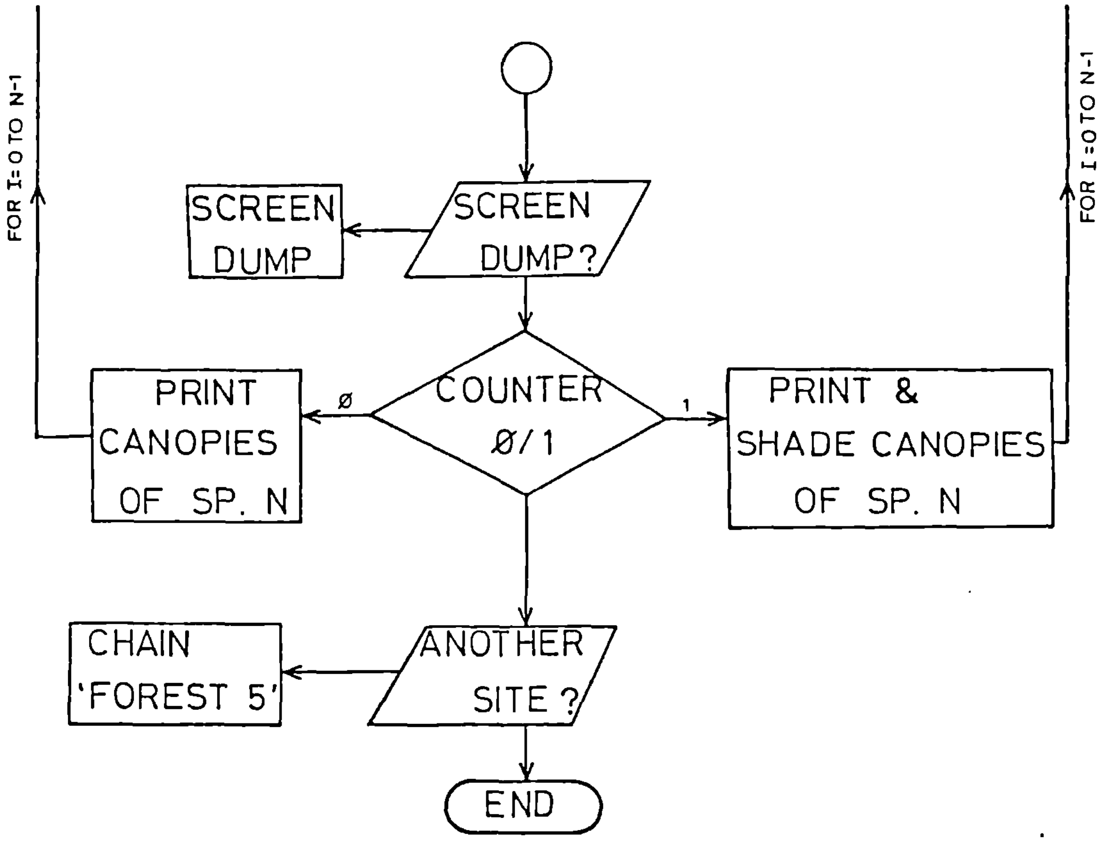
Notaris aethiops F.

Phyllobius or *Polydrusus* sp.

APPENDIX 4: PROGRAM 'FOREST 5' FLOW CHART




CHAIN PROGRAM "CIRCLE"
*LOAD SCREEN DUMP ROUTINE
MODE 0
SET GRAPHICS ORIGIN
SET TEXT WINDOW
RECALL SPP. & CO-ORD DATA
PRINT CANOPY CIRCLES OF ALL TREES
PRINT LIMIT OF SURVEY
SHADE NEXT TAXON? COUNTER SET 0/1


FOR I=0 TO N-1
SCREEN DUMP
SCREEN DUMP?
PRINT CANOPIES OF SP. N
0
COUNTER 0/1
1
PRINT & SHADE CANOPIES OF SP. N
FOR I=0 TO N-1
CHAIN 'FOREST 5'
ANOTHER SITE ?
END

APPENDIX 5: THE POLLEN TOTALS FROM MODERN ANALOGUE SITES

ANALOGUE SITES	TOTAL DRYLAND POLLEN	TOTAL POLLEN AND SPORES
ANSTON 1	376	376
ANSTON 2	328	330
ANSTON 3	314	318
ANSTON 4	371	373
FLAMBOROUGH 2	403	404
FLAMBOROUGH 5	350	353
FORDON 1	427	427
FORDON 5	322	325
FORDON 7	333	333
FORDON 8	357	359
FORDON 9	306	306
KINGSWOOD 1	314	316
KINGSWOOD 2	522	533
KINGSWOOD 3	303	321
KINGSWOOD 4	310	314
KINGSWOOD 5	365	365
KIPLINGCOTES 3	470	470
KIPLINGCOTES 5	308	308
KIPLINGCOTES 6	300	300
K'COTES SPRING 1	352	352
K'COTES SPRING 2	312	312
K'COTES SPRING 3	331	331
K'COTES SPRING 4	444	445
K'COTES SPRING 5	311	311

Appendix 5

ANALOGUE SITES	TOTAL DRYLAND POLLEN	TOTAL POLLEN AND SPORES
K'COTES SPRING 6	300	302
LITTLEWOOD 1	415	695
LITTLEWOOD 2	340	355
LITTLEWOOD 3	304	511
LITTLEWOOD 4	300	2100
NORTH NEWBALD 3	351	356
NORTH NEWBALD 5	314	374
PULFIN BOG 1	300	314
WHARRAM PERCY 1	504	981
WILLOW GARTH 1	464	467

APPENDIX 6: POLLEN COUNT TOTALS FROM WILLOW GARTH

UNCORRECTED DEPTH (cm)	TOTAL DRYLAND POLLEN	TOTAL POLLEN AND SPORES
0 - 4	300	300
4 - 6	306	306
6 - 8	308	308
8 - 10	306	352
10 - 12	357	408
12 - 14	191	241
14 - 16	393	433
16 - 18	332	475
18 - 20	337	460
20 - 22	317	450
22 - 24	191	335
24 - 26	353	501
26 - 28	305	449
28 - 30	320	411
30 - 32	305	400
32 - 34	311	411
34 - 36	363	300
36 - 38	393	478
38 - 40	317	385
40 - 42	307	352
42 - 44	304	383
44 - 46	310	348
46 - 48	303	349
48 - 50	304	363

UNCORRECTED DEPTH (cm)	TOTAL DRYLAND POLLEN	TOTAL POLLEN AND SPORES
50 - 52	510	617
52 - 54	318	388
54 - 56	302	432
56 - 58	317	444
58 - 60	321	440
60 - 61	354	806
61 - 62	311	894
62 - 63	310	1092
63 - 64	301	1259
64 - 65	150	752
65 - 66	312	1210
66 - 67	711	1045
67 - 68	332	642
68 - 69	377	586
69 - 70	309	677
70 - 71	328	633
71 - 72	300	711
72 - 73	448	654
73 - 74	426	661
74 - 75	407	854
75 - 76	400	746
76 - 77	440	519
77 - 78	486	526
78 - 79	482	522
79 - 80	609	655
80 - 81	584	706

UNCORRECTED DEPTH (cm)	TOTAL DRYLAND POLLEN	TOTAL POLLEN AND SPORES
81 - 82	750	906
82 - 83	513	1188
83 - 84	464	1487
84 - 85	344	911
85 - 86	576	1043
86 - 87	505	1021
87 - 88	515	2275
124 - 128	317	792
128 - 132	452	510
132 - 136	541	609

REFERENCES

Andersen, S.T. (1970). The relative pollen productivity and pollen representation of north European trees and correlation factors for tree pollen spectra. Danm. Geol. Unders. Raekke 2, 96, 1-99.

Andersen, S.T. (1973). The differential pollen productivity of trees and its significance for the interpretation of a pollen diagram from a forested region. In Quaternary Plant Ecology (eds H.J.B. Birks and R.G. West). Blackwell, Oxford.

Andersen, S.T. (1978a). Local and regional vegetational development in eastern Denmark in the Holocene. Danm. Geol. Unders., Arbog, 1976, 5-27.

Andersen, S.T. (1978b). Identification of wild grass and cereal pollen. Danm. Geol. Unders., Arbog 1978, 69-92.

Andersen, S.T. and Bertelsen, F. (1972). Scanning electron micrograph studies of pollen of cereals and other grasses. Grana, 12, 79-86.

Andrew, R. (1984). A practical pollen guide to the British flora. Quaternary Research Association, Technical Guide, 1,

Ashbee, P. and Smith, I.F. (1966). The date of Windmill Hill Long Barrow. Antiquity, 40, 299

Atkinson, B.W. and Smithson, P.A. (1976). Precipitation. In The Climate of the British Isles (eds T.J. Chandler and S. Gregory).pp 129-182. Longman, Lond. and N.Y.

Balfour-Brown, F. (1958). British Water Beetles, III. The Royal Society, London. 210 pp.

Ball, D.F. (1964). Loss on ignition as an estimate of organic matter and organic carbon in non-calcareous rocks. J. Soil Sci., 15, 84-92

Baker, C.A., Moxey, P.A. and Oxford, P.M. (1978). Woodland continuity and change in Epping Forest. Field Studies, 4, 645-669.

Barber, K.E. (1976). History of Vegetation. In Methods in Plant Ecology (ed. S.B. Chapman). Blackwells, Oxford.

Bartley, D.D. (1962). The stratigraphy and pollen analysis of lake deposits near Tadcaster, Yorkshire. New Phytol., 61, 277-287.

Beals, E.W. (1973). Ordination; mathematical elegance and ecological naivete. J. Ecol., 61, 23-35.

Beckett, S.C. (1975). The Late Quaternary Vegetational History of Holderness, Yorkshire. Unpubl. Ph. D. thesis, University of Hull.

Beckett, S.C. (1981). Pollen diagrams from Holderness, North Humberside. J. Biogeog., 8, 177-198.

Behre, K-E, (1981). The interpretation of anthropogenic indicators on pollen diagrams. Pollen Spores, 23, 225-245.

Bell, F.G. (1969). The occurrence of southern steppe and halophyte elements in Weichselian (full glacial) floras from southern England. New Phytol., 68, 913-921.

Bennett, K.D. (1983a). Devensian late-glacial and Flandrian vegetational history at Hockham Mere Norfolk, England. I. Pollen percentages and concentrations. New Phytol, 95, 457-487.

Bennett, K.D. (1983b). Devensian late-glacial and Flandrian vegetational history at Hockham Mere Norfolk, England. II. Pollen accumulation rates. New Phytol., 95, 489-504.

Benninghoff, W.S. (1962). Calculation of pollen and spore density in sediments by addition of exotic pollen in known quantities. Pollen Spores, 4, 332-333.

Benninghoff, W.S. and Kapp, R.O. (1962). Suggested notations to indicate identification status of fossil pollen. Pollen Spores, 4, 332.

Benzecri, J.P. (1969). Statistical analysis as a tool to make patterns emerge from data. In Methodologies of Pattern Recognition (ed S. Watanabe). Academic Press, N.Y..

Berglund, B.E. (ed) (1979). Palaeohydrological changes in the temperate zone in the last 15000 years. Guide to project 158B. International Geological Correlation Programme. Lund.

Berglund, B.E. and Malmer, N. (1971). Soil conditions and late-glacial stratigraphy. Geolog. Foren. Forhandl., 93, 575

Beug, H.J. (1961). Leitfaden der Pollenbestimmung fur Mitteleuropa und Angrenzende Gebeite. Lief 1. Gustav Fischer Verlag, Stuttgart.

Birks, H.H. (1973). Modern macrofossil assemblages in lake sediments in Minnesota. In Quaternary Plant Ecology (ed H.J.B.Birks and R.G.West). Blackwell, Oxford.

Birks, H.J.B. (1968). The identification of Betula nana pollen. New Phytol., 67, 309-314.

Birks, H.J.B. (1973). Past and Present Vegetation of the Isle of Skye - a Palaeoecological Study. Cambridge University Press.

Birks, H.J.B. and Birks, H.H. (1980). Quaternary Palaeoecology. Arnold, London. 289 pp.

Blackburn, K.B. (1952). The dating of a deposit containing an elk skeleton found at Neasham near Darlington, County Durham. New Phytol., 51, 364-377.

Bonny, A.P. (1972). A method for determining absolute pollen frequencies in lake sediments. New Phytol., 71, 391-403.

Bonny, A.P. (1976). Recruitment of pollen to the seston and sediment of some Lake District lakes. J. Ecol., 64, 859-887.

Bonny, A.P. (1978). The effect of pollen recruitment processes on pollen distribution over the sediment surface of a small lake in Cumbria. J. Ecol., 66, 385-416

Bradley, R. (1978). The Prehistoric Settlement of Britain. Routledge and Kegan Paul, London.

Bradshaw, R.H.W. (1981a). Modern pollen representation factors for woods in south-east England. J. Ecol., 69, 45-70.

Bradshaw, R.H.W. (1981b). Quantitative reconstruction of local woodland vegetation using pollen analysis from a small basin in Norfolk, England. J. Ecol., 69, 941-955.

Bradshaw, R.H.W. and Webb, T. (1985). Relationships between contemporary pollen and vegetation data from Wisconsin and Michigan, U.S.A.. Ecology, 66, 721-737.

Braun-Blanquet, J. (1932). Pflanzensoziologie. Springer, Wien.

Braun-Blanquet, J. (1951). Pflanzensoziologie, 2nd edn.. Springer, Wien.

Bray, J.R. and Curtis, J.T. (1957). An ordination of the forest communities of southern Wisconsin, Ecol. Monogr., 27, 325-349.

Brookes, D. and Thomas, K.W. (1967). The distribution of pollen grains on microscope slides. I. The non-randomness of the distribution. Pollen Spores, 9, 621-629.

Brown, A.P. (1971). The Empetrum pollen record as a climatic indicator in the late Weichselian and early Flandrian of the British Isles. New Phytol., 70, 841-849.

Buckland, P.C. (1984). North-west Lincolnshire 10000 years ago. In A Prospect of Lincolnshire (eds N.Field and A.White).

Buckland, P.C. and Edwards, K.J. (1984). The longevity of pastoral episodes of clearance activity in pollen diagrams: the role of post-occupation grazing. J. Biogeog., 11, 243-250.

Burleigh, R. and Kerney, M.P. (1982). Some chronological implications of a fossil mollusca assemblage from a Neolithic site at Brook. Kent, England. J. Arch. Sci., 9, 29-38.

Caratini, S. (1981). Pre-conference abstracts of the 5th International Conference of Palynology. Cambridge, England.

Care, V. (1983). The production and distribution of Mesolithic axes in southern England. Proc. Prehist. Soc., 49, 93-103.

Carr, O. (1983). The influence of grazing on pollen production in upland grasslands. Unpubld. Dissertation, Univ. of Hull.

Catt, J.A. (1978). The contribution of loess to soils in lowland Britain. In The Effect of Man on the Landscape: the Lowland Zone (eds S. Limbrey and J.G. Evans). Counc. Br. Archaeol. Res. Rep., 21.

Catt, J.A. (1981). British pre-Devensian glaciations. In The Quaternary in Britain (eds J. Neale and J.R. Flenley). Pergammon, Oxford.

Catt, J.A., Weir, A.H. and Madgett, P.A. (1974). The loess of eastern Yorkshire and Lincolnshire. Proc Yorks. Geol. Soc., 40, 23-39.

Clapham, A.R. (1940). The role of Bryophytes in the calcareous fens of the Oxford district. J. Ecol., 28, 71-80.

Clapham, A.R., Tutin, T.G. and Warburg, E.F. (1962). Flora of the British Isles. Cambridge University Press.

Clapham, A.R., Tutin, T.G. and Warburg, E.F. (1983). Excursion Flora of the British Isles. 3rd edn. Cambridge University Press.

Clark, J.G.D. (1936). The Mesolithic Settlement of Northern Europe. Cambridge University Press.

Clark, J.G.D. (1954). Excavations at Star Carr. An Early Mesolithic Site at Seamer, Near Scarborough, Yorkshire. Cambridge University Press.

Clark, J.G.D. and Godwin, H. (1956). A Maglemosian site at Brandesburton, Holderness, Yorkshire. Proc. Prehist. Soc., 22, 6-22

Coles, J.M. and Orme, B.J. (1983). Homo sapiens or Castor fiber? Antiquity, 57, 95-102.

Connah, G. and McMillan, N.F. (1964). Snails and archaeology. Antiquity, 38, 62-64.

Connolly, A.P. and Dahl, E. (1970). Maximum summer temperature in relation to the modern and Quaternary distributions of certain arctic-montane species in the British Isles. In Studies in the Vegetational History of the British Isles (eds D.Walker and R.G.West).

Conway, V.M. (1938). Studies in the autecology of Cladium mariscus. R.Br.5. The distribution of the species. New Phytol., 37, 312-328.

Conway, V.M. (1942). Biological flora of the British Isles: Cladium mariscus (L).R.Br.. J. Ecol., 30, 211-216. University Press.

Coope, G.R. (1970). Interpretations of Quaternary insect fossils. Ann. Rev. Entomology, 15, 97-120.

Coope, G.R. (1977). Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (last) cold stage. Phil. Trans. R. Soc. B, 280, 313-348.

Coope, G.R. and Brophy, J.A. (1972). Late Glacial environmental changes indicated by a coleopteran succession from North Wales. Boreas, 1, 97-142.

Coope, G.R., Shotton, F.W. and Strachan, I. (1961). A late Pleistocene fauna and flora from Upton Warren Worcestershire. Phil. Trans. R. Soc. B, 244, 379-421.

Cornish, M.W. (1954). The origin and structure of grassland types of the central North Downs. J. Ecol., 42, 359-374.

Cornwall, I.W. (1963). The environment. Appendix I, pp 200-201 in Manby, T.G. (1963). The excavation of Willerby Wold Long Barrow, East Riding of Yorkshire. Proc. Prehist. Soc., 29, 173-205.

Cottam, G., Goff, F.G. and Whittaker, R.H. (1973). Winsconsin comparative ordination. In Handbook of Vegetation Science. 5. Ordination and Classification of Communities (ed R.H. Whittaker). Junk, the Hague.

Crackles, F.E. (1968). Some plant associations of the River Hull Valley. East Yorkshire Field Studies, 1, 13-24.

Crackles, F.E. (1973). Seeking to understand the flora of the East Riding of Yorkshire. The Naturalist, 1974, 1-17.

Crackles, F.E. (1977). Biosystematic and taxonomic studies of populations of Calamagrostis stricta, C. canescens and their hybrids. Unpublished M.Sc. Thesis University of Hull.

Cranfield, R. (1941). Application of line interception in sampling range vegetation. J. Forest, 39, 388-394.

Curtis, J.T. (1959). The vegetation of Winsconsin: An ordination of plant communities. University of Winsconsin, Madison.

Curwen, E.C. (1938). Air Photography and the Evolution of the Corn-Field. Black, London.

Cushing, E.J. (1967). Late-Wisconsin pollen stratigraphy and the glacial sequence in Minnesota. In Quaternary Palaeoecology (eds E.J.Cushing and H.E.Wright). Yale University Press.

Davis, M.B. (1963). On the theory of pollen analysis. Am. J. Sci., 261, 897-912

Davis, M.B., Brubaker, L.B. and Beiswenger, J.M. (1971). Pollen grains in lake sediments: pollen percentages in surface sediments from southern Michigan. Quat. Res., 1, 450-467.

Davis, M.B., Brubaker, L.B. and Webb, T. (1973). Calibration of absolute pollen influx. In Quaternary Plant Ecology (eds H.J.B.Birks and R.G.West). Cambridge University Press.

Davis, R.B., Bradstreet, T.E., Stuckenrath, R. and Borns, H.W. (1975). Vegetation and associated environments during the past 14000 years near Moulton Pond, Maine. Quat. Res., 5, 435-465.

Deevey, E.S., Gross,, M.S.,Hutchinson, G.E. and Krabill, H.L. (1965). The natural C^{14} contents of material from hard water lakes, National Academy of Science Proc., 40, 285-288.

Dennell, R.W. (1983). European Economic Prehistory, a New Approach. Academic Press, London.

Dickson, J.H. (1973). Bryophytes of the Pleistocene. Cambridge University Press.

Digerfeldt, G. (1977). Palaeoecological studies of the recent development of Lake Vaxjosjou. II. Settlement and landscape development. Archiv fur Hydrobiologie, 79, 465-477.

Dimbleby, G.W. (1957). Pollen analysis of terrestrial soils. New Phytol., 56, 12-28.

Dimbleby, G.W. (1961). The ancient forest of Blackamore. Antiquity, 35, 123-128.

Dimbleby, G.W. (1962). The Development of British Heathlands and Their Soils. Oxford Forestry Mem., 23.

Dimbleby, G.W. (1963). Pollen analysis of a mesolithic site at Addington, Kent. Grana, 4, 140-148.

Dimbleby, G.W. (1967). Plants and Archaeology. Baker, London.

Evans, J.G. and Dimbleby, G.W. (1976). Appendix I: The pre-barrow environment. In Manby, T.G. (1976). The excavation of Kilham Long Barrow, East Riding of Yorkshire. Proc. Prehist. Soc., 42, 150-159.

Evans, P. (1975). The intimate relationship: an hypothesis concerning pre-Neolithic land use. In The Effect of Man on the Landscape: the Highland Zone. (eds. J.G.Evans, S. Limbrey, and H. Cleere). C.B.A. Res. Rep., 11.

Evans, R. (1976). Observations on a stripe pattern. Biul. Peryglac., 25, 9-22.

Faegri, K. (1971). The preservation of sporopollenin membranes under natural conditions. In Sporopollenin. (eds J.Brooks, P.R. Grant, M. Muir, P. van Gijzel and G. Shaw). Academic Press.

Faegri, K. and Iversen, J. (1975). Textbook of Pollen Analysis. Blackwell.

Farrow, E.P. (1917). On the ecology of the vegetation of Breckland (Norfolk and Suffolk). J. Ecol., 5, 1-18

Firbas, F. (1949). Spat-und Nacheiszeitliche Waldgeschichte Mitteleuropas Nordlich der Alpen, Vol 1. Fischer, Jena.

Fitter, A. (1978). An Atlas of Wild Flowers of Britain and Northern Europe. Cambridge University Press. 272 pp..

Flenley, J.R. (1973). The use of modern pollen rain samples in the study of the vegetational history of tropical regions. In Quaternary Plant Ecology (eds H.J.B.Birks and R.G.West). Cambridge University Press.

Flenley, J.R. and King, S.M. (1984). Late Quaternary pollen records from Easter Island. Nature, Lond., 307, 47-50.

Dimbleby, G.W. and Evans, J.G. (1974). Pollen and land snail analysis of calcareous soils. J. Archaeol. Sci., 1, 117-133.

Earnshaw, J.R. (1973). The site of a mediaeval post mill and prehistoric site at Bridlington. Yorkshire Archaeol. J., 45, 19-40.

Edwards, K.J. (1982). Man, space and the woodland edge - speculations on the detection and interpretation of human impact in pollen profiles. In Archaeological Aspects of Woodland Ecology (eds S.Limbrey and M.Bell). B.A.R. Int. Ser., 146.

Edwards, K.J. and Hiron, K.R. (1984). Cereal pollen grains in pre-elm decline deposits; implications for the earliest agriculture in Britain and Ireland. J. Arch. Sci., 11, 71-80.

Ellis, S. (1981). Patterned ground at Wharram Percy, North Yorkshire: Its origin and palaeoenvironmental implications. In The Quaternary in Britain (eds J.Neale and J.R.Flenley). Pergammon, Oxford.

Erdtman, G., Berglund,B. and Praglowski, J. (1961). An Introduction to Scandinavian Pollen Flora. Almqvist and Wiksell, Stockholm. **

Evans, J.G. (1971). Habitat change on the calcareous soils of Britain: the impact of Neolithic man. In Economy and Settlement in Neolithic and Early Bronze Age in Britain and Europe. (ed D.D.A. Simpson). University Press, Leicester.

Evans, J.G. (1972). Land Snails in Archaeology. Seminar Press, London.

Floyd, D.A. and Anderson, J.E. (1982). A new point interception frame for estimating cover of vegetation. Vegetatio, 50, 185-186.

Gauch, H.G. (1982). Multivariate Analysis in Community Ecology. Cambridge University Press. 298 pp..

Gauch, H.G., Whittaker, R.H. and Wentworth, T.R. (1977). A comparative study of reciprocal averaging and other ordination techniques. J. Ecol., 65, 157-174.

Gauch, H.G. and Whittaker, R.H. (1981). Hierarchical classification of community data. J. Ecol., 69, 537-557.

Girling, M. and Greig, J.R. (1977). Palaeoecological investigations of a site at Hampstead Heath, London. Nature, Lond., 268, 45-47.

Glob, P.V. (1965). The Bog People: Iron Age Man Preserved. Faber,London.

Godwin, H. (1940). Pollen analysis and forest history of England and Wales. New Phytol., 39, 370-400.

Godwin, H. (1943). Coastal peat beds of the British Isles and North Sea. J. Ecol., 31, 199-247.

Godwin, H. (1944). Age and origin of the Breckland heaths of East Anglia. Nature, Lond., 154, 6-7.

Godwin, H. (1962). Vegetational history of the Kentish chalk downs as seen at Wingham and Frogholt. Veroff. Geobot. Inst. Rubel., 37, 83-89.

Godwin, H. (1975). The History of the British Flora. 2nd edn Cambridge University Press.

Goodall, D.W. (1953). Objective methods for the classification of vegetation. I. The use of positive interspecific correlation. Australian J. Bot., 1, 39-63.

Goodall, D.W. (1954). Vegetational classification and vegetational continua. Angew. PflanzSoz., 1, 168-182.

Gordon, A.D. and Birks, H.J.B. (1972). Numerical methods in Quaternary Palaeoecology. I. Zonation of pollen diagrams. New Phytol., 71, 961-979.

Gordon, A.D. and Birks, H.J.B. (1974). Numerical methods in Quaternary Palaeoecology. II. Comparison of pollen diagrams. New Phytol., 73, 221-249.

Goudie, A.E. (1977). Environmental Change. Clarendon, Oxford.

Gould, R.A. (1982). To have and have not: the ecology of sharing among hunter-gatherers. In Resource Managers: North American and Australian Hunter-Gatherers (eds N.N.Williams and E.S.Hunn). Boulder: Westview Press.

GreatRex, P.A. (1983). Interpretation of macrofossil assemblages from surface sampling of macroscopic plant remains in mire communities. J. Ecol., 71, 773-792

Greig-Smith, P. (1964). Quantitative Plant Ecology. Butterworths, London.

Grohne, U. (1957). Die bedeutung des phasenkontrastverfahrens fur die pollenanlyse, dargelegt am beispiel der Gramineenpollen vom Getreidetyp. Photogr. Forsch, 7, 237-248.

Grosse-Brauckmann, G. (1974). Uber pflanczliche Makrofossilen mitteleuropaischer Torfe. 2. Weitere Reste (Fruchte und Samen, Moose u.a.) und ihre Bestimmungsmoglichkeiten. Telma, 4, 51-117.

Grubb, P.J., Green, H.E. and Merrifield, R.C.J. (1968). The ecology of chalk heath: its relevance to the calcicole - calcifuge and soil acidification problems. J. Ecol., 57, 175-212.

Gupta, S.K. and Polach, H.A. (1985). Radiocarbon Practices at ANU. ANU, Canberra.

Hafsten, U. (1956). Pollen analytic investigations on the late Quaternary development in the inner Oslofjord area. Arbok. Univ. Bergen, 8.

Hammond, R. and McCullagh, P. (1975). Quantitative Techniques in Geography. Oxford University Press.

Handel, S.N. (1976). Restricted pollen flow of two woodland herbs determined by neutron-activation analysis. Nature, Lond., 260, 4, 22-23.

Hare, F.K. (1959). A photo-reconnaissance survey of Labrador - Ungava Geographical Branch. Department of Mines and Technical Resources, Memoir 6.

Haslam, S.M., Sinker, C.A. and Wolseley, P.A. (1975). British water plants. Field Studies, 4, 243-351

Havinga, A.J. (1967). palynology and pollen preservation. Rev. Palaeobot. palynol., 2, 81-98.

Havinga, A.J. (1971). An experimental investigation into the decay of pollen and spores in various soil types. In Sporopollenin (eds J.Brooks, P.R.Grant, M.Muir, P.van Gijzel and G.Shaw). Academic Press.

Hill, M.O. (1973). Reciprocal Averaging. An eigenvector method of ordination. J. Ecol., 61, 237-249.

Hill, M.O. (1977). Use of simple discriminant functions to classify quantitative phytosociological data. In First Symposium on Data Analysis and Informatics (eds E.Diday, L.Lebart, J.P.Pages and R. Tomassone). Le Chesnay, France.

Hill, M.O. (1979a). TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics. Cornell University. N.Y.

Hill, M.O. (1979b). DECORANA - A FORTRAN program for detrended correspondance analysis and reciprocal averaging. Ecology and Systematics. Cornell University, N.Y.

Hill, M.O., Bunce, R.G.H. and Shaw, M.W. (1975). Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in scotland. J. Ecol., 63, 597-613.

Hill, M.O. and Gauch, H.G. (1980). Detrended Correspondance Analysis: An improved ordination technique. Vegetatio, 42, 47-58.

Hope-Simpson, J.F. (1941a). Studies in the vegetation of the English chalk. VII. Bryophytes and lichens in chalk grassland, with a comparison of their ocurrence in other calcareous grasslands. J. Ecol., 29, 107-116.

Hope-Simpson, J.F. (1941b). Studies in the vegetation of the English chalk. VIII. A second survey of the chalk grasslands of the South Downs. J. Ecol., 29, 217-267.

Howe, S. and Webb, T. (1983). Calibrating pollen data in climatic terms: improving the methods. Quat. Sci. Rev., 2, 17-51.

Huntley, B. and Birks, H.J.B. (1983). An Atlas of Past and Present Pollen Maps for Europe: 0 - 13000 years Ago. C.U.P., Cambridge

Hurst, J.G. (1979). 'Wharram' a study of settlement on the Yorkshire Wolds.The Society for Mediaeval Archaeology Monograph Series, 8.

Iversen, J. (1941). Landnam i Danmarks Stenalder. Danm. Geol. Unders. Ser., 4, 66, 20-68.

Iversen, J. (1949). The influence of prehistoric man on vegetation. Danm. Geol. Unders. Ser., 4, 3 (6), 1-25.

Iversen, J. (1956). Forest clearance in the Stone Age. Sci. Amer., 194, 36-41.

Jacobi, R.M. (1978). Population and landscape in Mesolithic lowland Britain. In The Effect of Man on the Landscape: the Lowland Zone (eds S. Limbrey and J.G Evans). C.B.A. Res. Rep., 21.

Jacobson, G.L. and Bradshaw, R.H.W. (1981). The selection of sites for palaeovegetational studies. Quat. Res., 16, 80-96.

Janssen, C.R. (1959). Alnus as a disturbing factor in pollen diagrams. Acta Botanica Neerlandia, 8, 55-58.

Janssen, C.R. (1967). A post glacial diagram from a small Typha swamp. Ecol Monogr., 37, 145-172

Janssen, C.R. (1973). Local and regional pollen deposition. In Quaternary Plant Ecology (eds H.J.B. Birks and R.G. West). pp. 31-42. Blackwell Scientific Publications, Oxford.

Janssen, C.R. (1984). Pollen transect across Minnesota peatland - Lake Myrtle. Ecol. Monogr., 54, 212-252.

Janus, H. (1982). The Illustrated Guide to Molluscs. Harold Stark Ltd., London.

Jarman, M.R. (1976). Early Animal Husbandry. Phil. Trans. R. Soc. B, 275, 85-97.

Jones, M.D. and Newell, L.C. (1948). Size variability and identification of grass pollen. J. Amer. Soc. of Agronomy, 40, 136-143.

Jones, R.L. (1976) Late Quaternary vegetational history of the North York Moors. IV. Seamer Carrs. J.Biogeogr., 3, 397-406.

Jones, R.L. (1977a). Late Quaternary vegetational history of the North York Moors. V. The Cleveland Dales. J. Biogeogr., 4, 353-362.

Jones, R.L. (1977b). Late Devensian deposits from Kildale, north-east Yorkshire. Proc. York. Geol. Soc., 41, 185-188.

Jones, R.L. and Gaunt, G.D. (1976). A dated Late Devensian organic deposit at Cawood, near Selby. The Naturalist, 1976, 121-124.

Keble Martin, W. (1974). The Concise British Flora. Rainbird, London. **

Keef, P.A.M., Wymer, J.J. and Dimbleby, G.W. (1965). A Mesolithic site on Ipping Comon, Sussex, England. Proc. Prehist. Soc., 31, 85-92.

Kelly, M.R. and Osborne, P.J. (1964). Two faunas and floras from the alluvium of Shustoke, Warwickshire. Proc. Linn. Soc. Lond., 176, 37-65.

Kendall, D.G. (1971). Seriation from abundance matrices. In Mathematics in the Archaeological and Historical Sciences. (eds F.R.Hodson, D.G.Kendall and P.Tautu).

Kenward, H.K., Hall, A.R., Jones, A.K.G. (1980). A tested set of techniques for the extraction of plant and animal macrofossils from waterlogged archaeological deposits. Science and Archaeology, 22, 3-15.

Kerney, M.P. (1963). Late-glacial deposits on the Chalk of south-east England. Phil. Trans. R. Soc. B, 246, 203-54

Kerney, M.P., Brown, E.H. and Chandler, T.J. (1964). The late-glacial and post-glacial history of the chalk escarpment near Brook, Kent. Phil. Trans. R. Soc. B, 248, 135-204.

Kerney, M.P. and Cameron, R.A.D. (1979). A Field Guide to the Land Snails of Britain and North-west Europe. Collins, London.

Kloet, G.S. and Hincks, W.D. (1945). A Check List of British Insects. Stockport.

Klotzli, G. (1970). Eichen-, Edellaub-, and Bruchwalder der Britischen Inseln. Schweizer. Z. Fortwesen, 5. 329-366.

Kershaw, K.A. and Looney, J.H.H., (1985). Quantitative and Dynamic Plant Ecology, 3rd edn. Edward Arnold, London.

Kramer, P.J. and Kozlowski, T.T. (1979). Physiology of Woody Plants. Academic Press, N.Y.

Lamb, H.F. (1984). Modern pollen spectra from Labrador and their use in reconstructing Holocene vegetational history. J. Ecol., 72, 37-60.

Lamb, H.F. (1985). Palynological evidence for post glacial change in the position of tree limit in Labrador. Ecol. Monogr., 55, 241-258.

Lamb, H.H. (1969). Climatic fluctuations. In World Survey of Climatology, 2, (ed H. Flohn). Elsevier, Amsterdam.

Lambert, C. (1964). Appendix 1: Late-glacial plant remains. In Kerney, M.P., Brown, E.H. and Chandler, T.J.. The late-glacial and post-glacial history of the chalk escarpment near Brook, Kent. Phil. Trans. R. Soc. B, 248, 135-204.

Levy, E.B. and Madden, E.A. (1933). The point method of pasture analysis. New Zealand J. Agric., 46, 267-269.

Lewin, J. (1969). The Yorkshire Wolds. A study in Geomorphology. Univ. Hull Occas. pap. Geogr., 11, 89 pp..

Liu, J., Tang, L., Qiao, Y., Head, M.J., Walker, D. (in press). Late Quaternary Vegetation history at Menghai, Yunnan Province, Southwest China. J. Biogeogr.

Loucks, O.L. (1962). Ordinating forest communities by means of environmental scalars and phytosociological indices. Ecol. Monogr., 32, 137-166.

McAndrews, J.H. (1966). Post glacial history of prairie, savanna, and forest in Northwestern Minnesota. Mem. Torrey. Bot. Club., 22, 1-72.

McVean, D.W. (1953). Ecology of Alnus glutinosa (L.) Gaertn., J. Ecol., 44, 195-218.

McVean, D.W. and Ratcliffe, D.A. (1962). Plant Communities of the Scottish Highlands. H.M.S.O., London.

Maher, L.J. (1972a). Nomograms for computing 0.95 confidence limits of pollen data. Rev. Palaeobot. Palynol., 11, 85-93.

Maher, L.J. (1972b). Absolute pollen diagram of Redrock Lake, Boulder County, Colorado. Quat. Res., 2, 531-553.

Manby, T.G. (1975). Neolithic occupation sites on the Yorkshire Wolds. *Yorks. Arch. J.*, *47*, 23-61.

Manby, T.G. (1976). The excavation of Kilham Long Barrow, East Riding of Yorkshire. *Proc. Prehist. Soc.*, *42*, 111-159

Mellars, P. (1975). Ungulate populations, economic patterns and the Mesolithic landscape. In *The Effect of Man on the Landscape: the Highland Zone* (eds J.G. Evans and S. Limbrey). C.B.A Res. Rep., 11, 49-56.

Merton, L.F.H. (1970). The woodlands of the Derbyshire limestone. *J. Ecol.*, *58*, 723-744.

Mittelbach, G.G. and Gross, K.L. (1984). Experimental studies of seed predation in old-fields. *Oecologia*, *65*, 7-13.

Moore, P.D. (1977). Ancient distribution of lime trees in Britain. *Nature*, Lond., *268*, 13-14.

Moore, P.D. and Webb, J.A. (1978). *An Illustrated Guide to Pollen Analysis*. Unibooks, London.

Morgan, A. (1973). Late Pleistocene environmental changes indicated by fossil insect faunas of the English Midlands. *Boreas*, *2*, 172-212.

Mosimann, J.E. (1965). Statistical methods for the pollen analyst: multinomial and negative multinomial techniques. In *Handbook of Palaeontological Techniques* (eds B. Kummel and D.M. Raup). W.H. Freeman.

Mueller-Dombois, D. and Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*. John Wiley & Sons, N.Y.

Neale, J. (1974), The Cretaceous. In The Geology and Mineral Resources of Yorkshire, (eds D.H.Rayner and J.E.Hemingway) Yorks. Geol. Soc., Leeds.

Noy-Meir, I. and Austin, M.P. (1970). Principal component ordination and simulated vegetational data. Ecology, 51, 551-552.

Oldfield, F. (1970). Some aspects of scale and complexity in pollen-analytically base palaeoecology. Pollen Spores, 12, 163-172.

Orlocci, L. (1966). Geometric models in Ecology. I. The theory and application of some ordination methods. J. Ecol., 54, 193-215.

Paul, C.R.C. (1975). The ecology of mollusca in ancient woodland. I. The fauna of Hayley Wood, Cambridgeshire. J. Conch., 28, 301-327.

Peck, R. (1973). Pollen budget studies in a small Yorkshire catchment. In Quaternary Plant Ecology (eds H.J.B.Birks and R.G.West). Blackwell.

Pennington, W. (1979). The origins of pollen in lake sediments: an enclosed lake compared with one receiving inflow streams. New Phytol., 83, 189-213.

Penny, L.F., Coope, G.R. and Catt, J.A. (1969). Age and insect fauna of the Dimlington silts, East Yorkshire. Nature (Lond.), 224, 65-67.

Perring, F.H. and Walters, S.M. (1962). Atlas of the British Flora. Bot. Soc. Brit. Isl., London.

Peterken, G.F. (1981). Woodland Conservation and Management. Chapman and Hall, London.

Pigott, C.D. (1969). The status of Tilia cordata and T. platyphyllos on the Derbyshire limestone. J. Ecol., 57, 491-504.

Pigott, C.D. and Walters, S.M. (1954). On the interpretation of the discontinuous distribution shown by certain British species of open habitats. J. Ecol., 42, 95-117.

Poore, M.E.D. (1955). The use of phytosociological methods in ecological investigations. II. Practical issues involved in an attempt to apply the Braun-Blanquet system. J. Ecol., 43, 245-269.

Poore, M.E.D. (1956). The use of phytosociological methods in ecological investigations. IV. General discussion of phytosociological problems. J.Ecol., 44, 28-50.

Praglowski, J.R. (1962). Notes on the pollen morphology of Swedish trees and shrubs. Grana Palynol., 3(2), 45-65.

Praglowski, J.R. and Wenner, C.G. (1968). The two Alnus species - in varve chronology, pollen analysis and radiocarbon dating. Stockh. Contr. Geol., 18, 1-75

Preece, R.C. and Robinson, J.E. (1984). Late Devensian and Flandrian environmental history of the Ancholme Valley, Lincolnshire: molluscan and ostracod evidence. J. Biogeog., 11, 319-352.

Prentice, I.C. (1985). Pollen representation, source area, and basin size toward a unified theory of pollen analysis. Quat. Res., 23, 76-86.

Punt, W. (1984). The northwest European flora (NEPF): Umbelliferae. Rev. Palaeobot. Palynol., 42, 155-363. **

Punt, W. and Malotaux, M. (1984). The northwest European pollen flora (NEPF): Cannabaceae, Moraceae and Urticaceae. Rev. Palaeobot. Palynol., 42, 23-44. **

von Post, L. (1925). Gotlands-agen (Cladium mariscus R.Br.) i Sveriges postarktikum. Ymer, 45, 295.

Rackham, O. (1980). Ancient Woodland, Its History, Vegetation and Uses in England. Arnold, Cambridge.

Rackham, O. (1983). A review of: Peterken, G. (1981). Woodland Conservation and Management. J. Ecol., 71, 658-660

Ratcliffe, D.A. (1977). A Nature Conservation Review: the Selection of Biological Sites of National Importance to Nature Conservation in Britain. Cambridge University Press.

Rawitscher, F. (1945). The hazel period in the post-glacial development of forests. Nature (Lond.), 156, 302-303.

Raynor, G.S., Hayes, J.V. and Ogden, E.C. (1974). Particulate dispersion into and within a forest. Boundary-Layer Meteorology, 7, 429-456.

Raynor, G.S., Hayes, J.V. and Ogden, E.C. (1975). Particulate dispersion from sources within a forest. Boundary-Layer Meteorology, 9, 257-277.

Renfrew, C. (1978). Trajectory discontinuity and morphogenesis: the implications of catastrophe theory for archaeology. Am. Antiq., 43, 203-222

Ritchie, J.C. (1974). Modern pollen assemblages near the arctic tree-line, MacKenzie delta region, Northwest Territories. Can. J. Bot., 52, 381-396.

Ritchie, J.C. (1977). The modern and late Quaternary vegetation of the Campbell-Dolomite uplands, near Inuvik, N.W.T. Canada. Ecol. Monogr., 47, 401-423.

Ritchie, J.C. and Lichti-Federovich, S. (1967). Pollen dispersal phenomenen in Arctic - Subarctic Canada. Rev. Palaeobot. Palynol., 3, 255-266.

Roux, I. and Leroi-Gourhan, A. (1965). Les defrichements de la periode atlantique. Bull. Soc. Prehist. Fr., 61, 309-315.

Rowell, T.A., Guarino, L. and Harvey, H.J. (1985). The experimental management of vegetation at Wicken Fen, Cambridgeshire. J. Appl. Ecol., 22, 217-227.

Rowell, T.K. and Turner, J. (1985). Litho- humic- and pollen stratigraphy at Quick Moss, Northumberland. J. Ecol., 73, 11-26.

Rowley, J.R. and Rowley, J. (1956). Vertical migration of spherical and aspherical pollen in a Sphagnum bog. Proc. Minn. Acad. Sci., 24, 29-30.

Rowley, J.R. (1960). The exine structure of "cereal" and "wild" type grass pollen. Grana Palynol., 2, 9-15.

Ryvarden, L. (1971a). Studies in seed dispersal. I. Trapping of diaspores in the alpine zone at Finse, Norway. Norwegian J. Bot., 18, 215-226.

Ryvarden, L. (1971b). Studies in seed dispersal. II. Winter dispersed species at Finse, Norway. Norwegian J. Bot., 22, 21-24.

Salisbury, F.B. and Ross, C.W. (1978). Plant Physiology 2nd edn. Wadsworth, U.S.A.

Scaife, R.G. (1980). Late Devensian and Flandrian Palaeoecological Studies in the Isle of Wight. Unpublished Ph.D. Thesis, University of London.

Seagrief, S.C. (1955). A Pollen Analytic Investigation of the Quaternary Period in Britain. Unpublished Ph.D. Thesis, University of Cambridge.

Shimwell, D. (1971a). Festuco-Brometea Br-Bl. and R. Tx 1943 in the British Isles: the phytogeography and phytosociology of limestone grasslands. I. General introduction; Xerobromion in England. Vegetatio, 23, 1-28.

Shimwell, D. (1971b). Festuco-Brometea Br-Bl. and R. Tx 1943 in the British Isles: the phytogeography and phytosociology of limestone grasslands. I. General introduction; Eu-Mesobromion in England. Vegetatio, 23, 29-60.

Sidaway, R. (1963). A buried peat deposit at Litton Cheney. Proceedings of the Dorset Natural History and Archaeological Society, 85, 78-86.

Simmons, I.G. (1969). Pollen diagrams from the North York Moors. New Phytol., 68, 807-827.

Simmons, I.G. (1981). Culture and environment. In The Environment in British Prehistory (eds I.G. Simmons and M. Tooley). Duckworth, London.

Simmons, I.G., Dimbleby, G.W. and Grigson, C. (1981). The Mesolithic. In The Environment in British Prehistory (eds I.G. Simmons and M.J. Tooley). Duckworth, London.

Simpkins, K. (1974). The Late-Glacial deposits at Glanllynnau, Caernarvonshire. New Phytol., 73, 605-618.

Smith, A.G. (1958). The content of some late Bronze Age and Early Iron Age remains from Lincolnshire. Proc. Prehist. Soc., 24, 78-84.

Smith, A.G. (1970). The influence of Mesolithic and Neolithic man on British vegetation: a discussion. In Studies in the Vegetational History of the British Isles (eds D. Walker and R.G. West). Cambridge University Press.

Smith, A.J.E. (1978). The Moss Flora of Britain and Ireland. Cambridge University Press.

Smith, C.A.B. (1966). Biomathematics, the principles of mathematics for students of biological and general science. I. Algebra, geometry, Calculus. Griffin, London.

Smith, C.J. (1980). The Ecology of the English Chalk. Academic Press, London.

Stockmarr, J. (1971). Tablets with spores used in absolute pollen analysis. Pollen Spores, 13, 615-621.

Straw, A. (1979a). An early Devensian glaciation in eastern England? Quaternary Newsletter, 28, 18-24.

Straw, A. (1979b). The geomorphological significance of the Wolstonian glaciation of eastern England. Trans. Inst. Br. Geogr., 4 (new series), 540-549.

Strickland, H.E. (1812). A General View of the Agriculture of East Yorkshire.

Sturludottir, S.A. and Turner, J. (1985). The elm decline at Pawlaw Mire: an anthropogenic interpretation. New Phytol., 99, 323-329.

Suggate, R.P. and West, R.G. (1959). The extent of the last glaciation in eastern England. Proc. R. Soc. B, 150, 263-283

Tansley, Sir A.G. (1939). The British Islands and Their Vegetation. Cambridge.

Tansley, Sir A.G. and Adamson, R.S. (1926) A preliminary survey of the chalk grasslands of the Sussex Downs. J. Ecol., 14, 1-32.

Tauber, H. (1965). Differential pollen dispersion and the interpretation of pollen diagrams. Danm. Geol. Unders., Ser II, 89, 1-69.

Tauber, H. (1977). Investigations of aerial pollen transport in a forested area. Dansk. Botanisk Arkiv, 32, 121 pp.

Thomas, A.E., Rawes, M. and Banner, W.J.L. (1957). The vegetation of the Pewsey Vale escarpment, Wiltshire. J. Grassland Soc., 12, 39-48.

Thomas, A.S. (1960). Changes in vegetation since the advent of myxamatosis. J. Ecol., 48, 287-306.

Thomas, A.S. (1963). Further changes in vegetation since the advent of myxamatosis. J. Ecol., 51, 151-186.

Thorley, A.J. (1971). An Investigation Into the Post-Glacial History of Native Tree Species in South-East England, Using the Pollen Analysis Technique. Unpublished Ph.D. Thesis, University of London.

Thorley, A.J. (1981). Pollen analytical evidence relating to the vegetational history of the chalk. J. Biogeogr., 8, 93-106.

Tindale, N.B. (1972). The Pitjandara. In Hunters and Gatherers Today (ed M.G. Biccieri). Holt, Rhinehart & Winston, N.Y.

Tinsley, H. and Smith, R.T. (1974). Surface pollen studies across a woodland/Heath transition and their application to the interpretation of pollen diagrams. New Phytol., 73, 547-565.

Tinsley, J. (1950). The determination of organic carbon in soils by dichromate mixtures. Trans. 4th Int. Cong. Soil Sci., 1, 161-164.

Tomlinson, P. (1984). Ultrasonic filtration as an aid in pollen analysis of archaeological deposits. Circaea, 2(3), 139-141.

Tout, D. (1976). Temperature. In The Climate of the British Isles (eds T.J. Chandler and S.Gregory).pp 96-128 Longman, Lond. and N.Y..

Troels-Smith, J. (1954). Erte bollekultur - Bondekultur. Aarb. Nord. Oldkynd. Hist. 1953, 5-62.

Troels-Smith, J. (1955). Karakterising af lose jordarter (characterisation of unconsolidated sediments.) Danm. Geol. Unders., Ser. IV, 3, 1-73.

Troughton, J.H., Wells, P.V. and Mooney, H.A. (1974). Photosynthetic mechanisms and palaeoecology from carbon isotope ratios in ancient specimens of C4 and CAM plants, Science, 185, 610-612.

Turner, J. (1962). The Tilia decline: an anthropogenic interpretation. New Phytol., 61, 328-341.

Turner, J. (1964). Anthropogenic factor in vegetation history. New Phytol., 63, 73-89.

Turner, J. (1965). A contribution to the history of forest clearance. Proc. R. Soc., B, 161, 343-354.

Turner, J. and Kershaw, A.P. (1973). A late and post-glacial pollen diagram from Cranberry Bog, near Beamish, County Durham. New Phytol., 72, 915-921

Walker, D. (1966). The Late Quaternary history of the Cumberland Lowland. Phil. Trans R. Soc., B, 25, 1-210.

Walker, D. (1972). Quantification in historical plant ecology. Proc. Australian Ecol. Soc., 6, 91-104.

Walker, D. and Godwin, Sir H. chapter 2. In Excavations at Star Carr. An Early Mesolithic Site at Seamer, Near Scarborough, Yorkshire. Clark, J.G.D. (1954). Cambridge University Press.

Washburn, A.L. (1979). Geocryology, Arnold, London.

Waton, P.V. (1982). A Palynological Study of the Impact of Man on the Landscape of Central Southern England with Special Reference to the Chalklands. Unpublished Ph.D. Thesis, University of Southampton.

Watson, E.V. (1969). British Mosses and Liverworts, 2nd edn. Cambridge University Press.

Watt, A.S. (1981a). A comparison of grazed and ungrazed grassland A in East Anglian Breckland. J. Ecol., 69, 499-508.

Watt, A.S. (1981b). Further observations on the effects of excluding rabbits from Grassland A in East Anglian Breckland: the pattern of change and factors affecting it (1936 - 1973). J. Ecol., 69, 509-536.

Watts, W.A. (1973). Rates of change and stability in vegetation in the perspective of long periods of time. In Quaternary Plant Ecology (eds H.J.B. Birks and R.G. West). Blackwell.

Webb, T., III, Laseski, R.A. and Bernabo, T.C. (1978). Sensing vegetational patterns with pollen data: choosing the data. Ecology, 59, 1151-1163.

Wells, T.C. (1969). Botanical aspects of conservation management of chalk grasslands. Biological Conservation, 2, 36-44.

West, R.G. (1968). Pleistocene Geology and Biology. Longman.

West, R.G. (1970). Pleistocene history of the British flora. In Studies in the Vegetational History of the British Isles (eds D. Walker and R.G. West). Cambridge.

Wheeler, B.D. (1980a). Plant communities of rich-fen systems in England and Wales. I. Introduction. Tall sedge and reed communities. J. Ecol., 68, 365-395.

Wheeler, B.D. (1980b). Plant communities of rich-fen systems in England and Wales. II. Communities of calcareous mires. J. Ecol., 68, 405-420.

Wheeler, B.D. (1980c). Plant communities of rich-fen systems in England and Wales. III. Fen meadow, fen grassland and fen woodland communities and contact communities. J. Ecol., 68, 761-788.

Whitman and Siggeirsson, (1954). Comparison of line interception and point contact methods in the analysis of mixed grass vegetation. Ecology, 35, 431-436.

Whittaker, R.H. (1962). Classification of natural communities. Botanical Review, 28, 1-239.

Whittle, A.W.R. (1980a). Two Neolithics? I. Current Archaeology, 6, 329-334.

Whittle, A.W.R. (1980b). Two Neolithics? II. Current Archaeology, 7, 371-373.

Williams, D. (1976). A Neolithic moss flora from Silbury Hill. J. Arch. Sci., 3, 267-270.

Williams, R.B.G. (1964). Fossil patterned ground in eastern England. Biul. Peryglac., 17, 311-335.

Wilton, W.C. (1965). The Forests of Labrador. Canada Forestry Service Publication 1066, Ottawa.

Winkworth, R.E. (1955). The use of point quadrats for the analysis of heathland. Australian J. Bot., 3, 68-81.

Wiseman, J. (1972). The environment (page 22). In Pacitto. A.L.. Rudston Barrow LXII the 1968 excavation. Yorks. Arch. J., 44, 1-22.

Wood, C.J. and Smith, E.G. (1978). Lithostratigraphical classification of the chalk in North Yorkshire, Humberside and Lincolnshire. Proc Yorks Geol. Soc., 42, 263-287.

Wright C.W. and Wright, E.V. (1942). The chalk of the Yorkshire Wolds. Proc Geol. Soc., 53, 112-127.

Wright, E.V. and Wright C.W. (1947). Prehistoric boats from North Ferriby, East Yorkshire. Proc. Prehist. Soc., 7, 114-138.

Wright, H.E. (1967). The use of surface samples in Quaternary pollen analysis. Rev. Palaeobot., Palynol., 2, 321-330.

** = Key utilise for identification not otherwise mentioned in text.