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Pollen analysis and community structure of Holocene forests: A regional palynological study of the Middle and Upper Postglacial from semi-subhydric alder carr sediments at Berdorf (Luxembourg)

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Key words: pollen extraction - pollen concentration - statistical analysis - ecology -postglacial forest development - community structure - population dynamics - interspecific competition - species replacement - succession - seed dispersal - fire -climatic change -archaeology - human activity - refuge habitat - relictual species -conservation

Main species: *Fagus* sp. - *Quercus* sp. - *Tilia* sp. - *Corylus* sp. - *Pinus* sp. - *Homo sapiens* - Cervidae

ABSTRACT

Forest trees produce plenty of pollen which after mixing in the atmosphere may become trapped in water bodies and incorporated into their sediments. Pollen of flowering plants are often identifiable to generic level, so cores taken from such suitable sediments may be analysed with respect to their fossil pollen content and give a sequence of changing abundances of local as well as regional plant taxa growing in the nearby area at a particular moment in time.

A pollen core covering about 8000 years was obtained from hydromorphic sediments of a small alder carr at Berdorf (Grand-Duchy of Luxembourg). The Holocene pollen record provided an opportunity to apply several recent developments concerning the extraction, representation and statistical analysis of pollen data.

The local hydroseral succession is described briefly while attention is focused mainly towards the role of interspecific competition, physical environmental factors and natural gap disturbances in determining the composition of past and present forest communities on a regional scale.

The role of *Tilia* as a major arboreal component during the Atlantic period is critically re-evaluated and it is suggested that steep sided valley slopes may have comprised quite distinct arboreal populations from those of valley bottoms or elevated plateaux. Furthermore the presence of several species notably *Pinus sylvestris,* presently growing in isolated stands scattered along rocky sandstone outcrops of the plateaux margins is claimed to be related to the nature of this refuge habitat, where relictual and hence native arboreal taxa may have survived in small populations until the present day.

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INTRODUCTION

Enclosed by the valleys of the rivers Sûre, Black Ernz and Aesbaach, the Berdorf plateau (see fig. 1) is part of an area of undulating relief, rising up to 370 m, that may be seen as intermediate between the countries southern lowlands and the heavily eroded hercynian mountain chain of the northern Ardennes massif.

Geologically, the latter consists of palaeozoic, metamorphous folded rocks from the Devonian while former is a northern extension of the Paris Basin, comprising mainly early Mezozoic fluvial deposits (Bundsandstein) overlain by a series of consolidated clastic and detrital sediments deposited during phases of marine ingressions in the Triassic and Jurassic.

The plateaux soils of the study area largely derive from the underlying sandstone bedrock with patches of Lias marls occurring more frequently towards the central parts, that is, away from the more exposed and eroded margins of the plateaux and valley borders.

Due to the nature and predominance of a sandy type of substrate, both of which are unfavourable to the preservation of organic micro- and macrofos-

sils, the apparent lack of suitable deposits for carrying out palaeo-environmental investigations is regrettable, particularily from an archaeological point of view.

It is not surprising therefore that pollen analytical work in the area has sofar mainly been concerned with sampling scarce peat deposits that are often of recent age or located at lower altitudes such as valley bottoms, where plant communities may be different from those of valley slopes or the plateaux.

In fact, the closest published pollen diagram to Berdorf comes from precipitated calcium carbonate deposits near the Aesbaach stream (Couteaux 1970). However, such concretionary spring deposits (travertine or tufa) may become interbedded with scree earths and often reveal interrupted pollen sequences.

It is somehow surprising that nobody sofar has seemed to bother sampling the sediments of several shallow waterlogged depressions to be found in the study area. Despite the fact that they do not always figure on national ordonance survey maps and are presently confined to wooded areas and may even temporarily dry out in summer, these basins are nevertheless well known to local people who generally refer to them as "Muer" (english "moor") and who have coined individual place names to some of them.

This study was undertaken in continuation of the excavation of a nearby mesolithic rock shelter site by researchers of the Prehistoric Society (Blouet et al 1984) to whom a knowledge of the regional vegetational history may be of great help in their attempts to interpret and reconstruct the socio-economic context of past human communities that evolved in this area.

Furthermore, the progressive disappeareance of these wetland sites as a result of natural silting aided by drainage for agricultural purposes and concerns about the lowering of the local water table following increased demands for quality water supplies are all reasons that justified investigating the organic mud deposits of these water holes before their destruction would render such analyses impossible.

1. MATERIALS AND METHODS

1.1. Field methods

For a stratigraphical investigation of the basin and in order to recover pollen samples from core sections, a 700 mm dutch auger fitted with extension rods was used that allowed to recover undisturbed core sections of 100 cm at a time.

A transect of borings was made along a previously aligned axis and sediment profiles were directly described in the field following that of Gardiner and Dackombe (1983). This enabled to demonstrate the uniformity of the sedimentary sequence and to locate the best coring place for the final pollen borehole. The so obtained core was entirely transferred into half-



Fig. 1. – Location of the pollen site within the study area

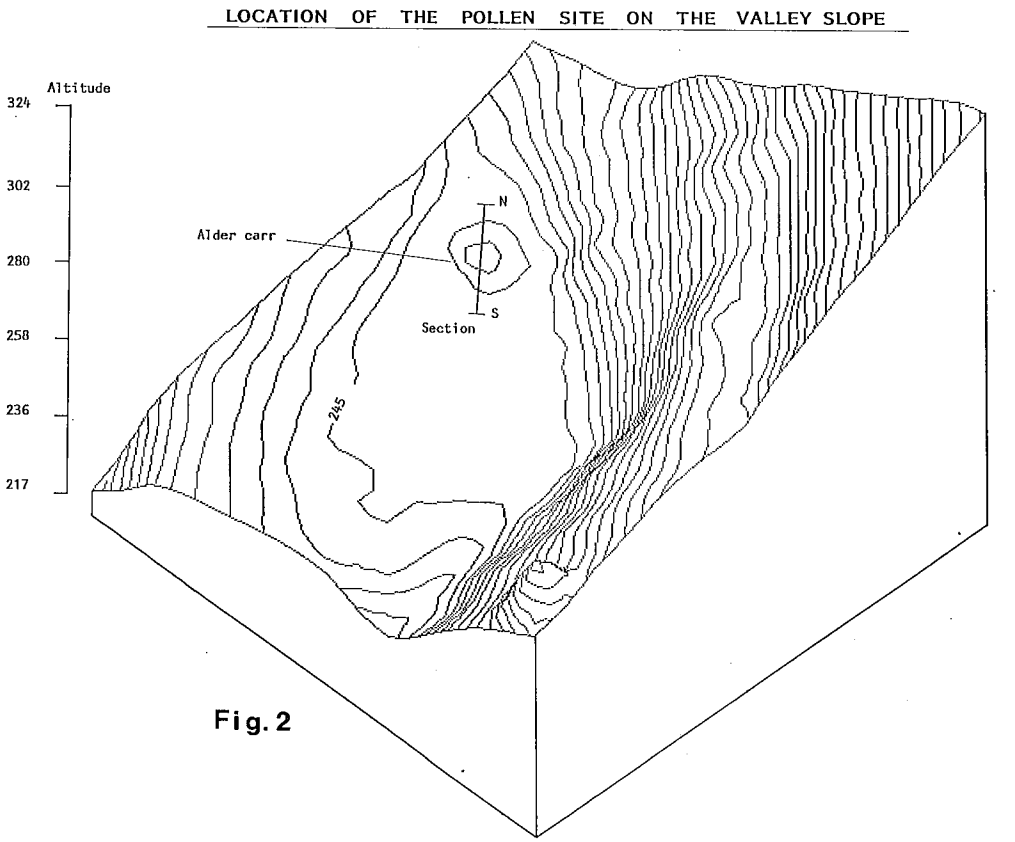


Fig. 2

sectioned plastic drain pipes, wrapped with cellophane and stored in a freezer at -20°C.

1.2. Laboratory methods

On return to the environmental laboratory, sediment samples of 1 cm^3 were removed from the central part of the core and preparation techniques followed those developed by pre-quaternary geologists working for the oil industry at the Geology Department of the University of Sheffield (Hunt 1985) and adapted to quaternary palynology by workers at the Archaeology Department.

Two tablets of exotic *Eucalyptus* sp., containing each about 1500 pollen grains to be used as tracers for estimating pollen concentration, were dissolved in hydrochloric acid, stained with Fuchsin and added to each sediment sample that had previously been homoginized in a small 150 ml Pyrex beaker, containing 125 ml of 5% Potassium Hydroxide. All preparations were then gradually brought to ebullition for 5 minutes on a sand heater before undergoing micropore filtration through nylon boulting cloths

with apertures of 100μ and 5μ. The latter being sufficiently small to retain Quaternary pollen and algal microfossils, while letting through a maximum of finer particles.

A fine but strong jet of filtered water was applied to break the surface tension and enable the water to drain through the cloth. Silts and other residual particles were separated from microfossils by gently swirling the aqueous suspension in a clock-glass. Former will fall out of suspension and accumulate at the bottom, while pollen grains and other lighter materials remain in suspension and can then be poured off or pippeted out and resuspended several times after disposing of the residue. This, until all silt particles have disappeared.

The final suspension was filtered again through a 5μ cloth and the remaining pollen concentrate could then be stained with 2 drops of Safranine and mounted in glycerine jelly on one slide per sample. Differential staining of the added exotic tracer grains and the fossil pollen facilitated the counting process which was carried out on a mechanical stage permetting regular scanning and traversing of slides under an optical light microscope at magnifications of x400. Pollen identification was done with reference to the pollen key of Moore and Webb (1977) and the departmental pollen collection.

This method which has now become a standard procedure in the univerities Archaeology Department is a very good alternative or supplement to conventional pollen extraction techniques (Acetolysis, Hydrofluoric acid maceration) that makes pollen analysis less time consuming (10 minutes per sample), safer (reduced handling of noxious chemicals) and cheaper (less chemicals and little expensive equipement). Preparations obtained in this way are also comparatively "cleaner" thus making the identification and counting of pollen easier. Unlike acetolysis, this technique has not yet been shown to selectively destroy spores and pollen of certain taxa (Erdtman 1952). Other microfossils such as diatoms, dinoflagellates, algal remains and fungal spores are also preserved and may be studied using the same slide preparation.

RESULTS

2.1 The pollen diagram site

2.1.1 Location and site description

The "Dauwelsmuer" (49°48' North, 6°19' East) is situated ca 2 km S-W to the village of Berdorf, on a concave slope segment of the valley of the river Black Ernz at an altitude of 245 m (see fig. 2).

The bog fills an oval depression ca 50 m long and 40 m wide, bordered to the S-E by a relatively steep micro-cliff, exposing a loosely consolidated colluvial sandstone matrix containing large boulders, several of which have become detached and are scattered along the edge of the site. The pollen core was obtained in August 1985, at a time when the water level had dropped below the muddy ground surface, revealing large rotten tree stems with a thick, partly decomposed twig and leaf litter covering the mire.

For most of the year the basin is flooded to a depth up to 1 m and depending upon prevailing climatic conditions, it may dry out for a short period during the summer.

The small submerged plain supports ash and alder trees, the swollen stems of the latter being colonized by bryophytes notably *Polystichum sp.* The presence of several mosses such as *Mnium sp.* and *Thuidium sp.* may be indicative of a calcium enriched substrate. The death of several trees along the rim of the depression may be related to a rising of the flooded area consecutive to natural silting. Mixed deciduous woodland (beech, oak, hornbeam, sycamoré) extends close to the margins of the alder carr where a fringing ground vegetation including policeman's helmet *(Impatiens glandulifera),* various ferns, grasses and few sedges, have invaded the shallower parts of the site.

In addition to precipitation, the basin is supplied in cold water by runoff from the steep sided valley slope. Several springs are found at this altitude on the hillsides of the valleys and the high calcium content of the water is generally believed to originate from leaching of sandstone cement and calcareous clays through which percolating water finds its way. Isolated tufa deposits with ongoing calcium carbonate precipitation are quite a common phenomena in the region and have also been found in proximity to this site.

Human activity was not directly noticeable although the "fresh" appearance of the micro-cliff an the presence of boulders of a high quality, fine grained and hardly cemented type of sandstone ressembling quartzite (locally known as "Bengléck") may be taken as signs of a small scale quarrying activity that may have lasted until world war II.

The two bordering forest trails seem to follow the natural topography and although one of them required filling up the western margin of the depression with building debris, no further earthworks or therelike anthropogenic alterations were noticed.

2.1.2 Lithology

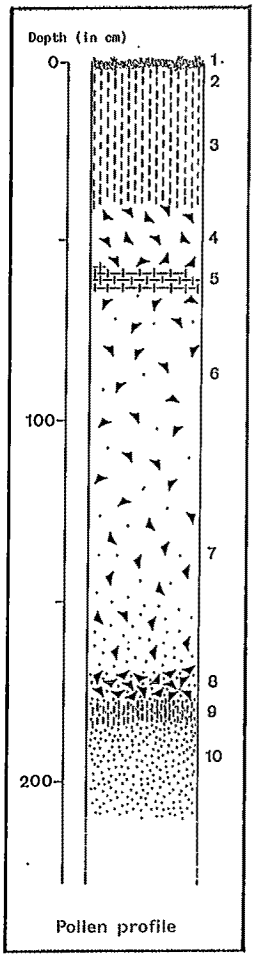


Fig. 3

Pollen borehole stratigraphy (see fig. 3)

0 - 1 cm	Fresh litter with partly decomposed leaves and twigs.
1 - 8 cm	Brownish-gray loam with fine fragments of organic remains. Sharp boundary to the next horizon.
8 - 38.5 cm	Grayish brown clay loam with finer organic particles and common medium sized and prominent reddish mottles. Extremely sharp boundary to next horizon.
38.5-55.5 cm	Dark coloured reddish brown woody peat without any sand particles. Dry and compact consistency. Sharp boundary to next horizon.
55.5-64 cm	Grayish brown loamy clay with small organic particles. Clear boundary to next horizon.
64-112 cm	Brown-reddish woody peat. Very compact and containing small amounts of sand grains. Changing progressively into a
112-172 cm	Dark reddish-brown woody peat containing an increasing fraction of sand towards the basal zone.
172-178 cm	Very compact brown sandy peat.
178-182 cm	Grayish-red loamy sand changing gradually into a
182-210 cm	Yellowish-gray sand that becomes very 'fluid' and does not hold well in the sampling device.

Simplified site stratigraphy: Graphically shown on fig. 4.

2.2 The pollen diagram

2.2.1 Construction of the pollen diagram

Pollen was counted until a minimum of 200 arboreal pollen grains (AP) was counted (excluding Corylus) or 300 total dry land pollen (TDLP) had been reached for each level.

The total pollen and spore sum includes that of trees and shrubs and that of aquatic and terrestrial plants. Results were expressed as percentages of total dry land pollen (excluding *Alnus* and *Salix)* on a percentage diagram (see fig. 5).

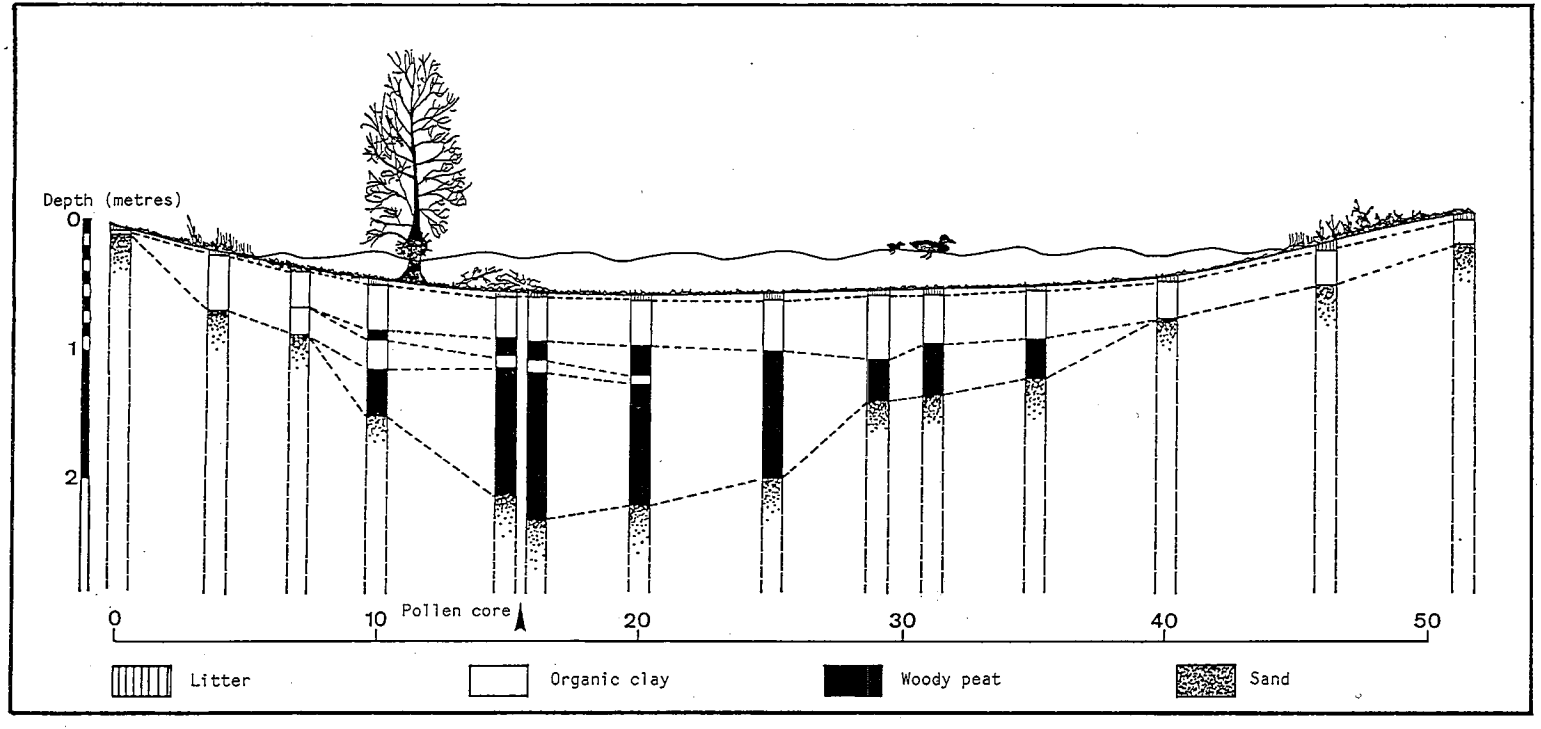


Fig. 4 Simplified site stratigraphy of the alder carr (South-North section).

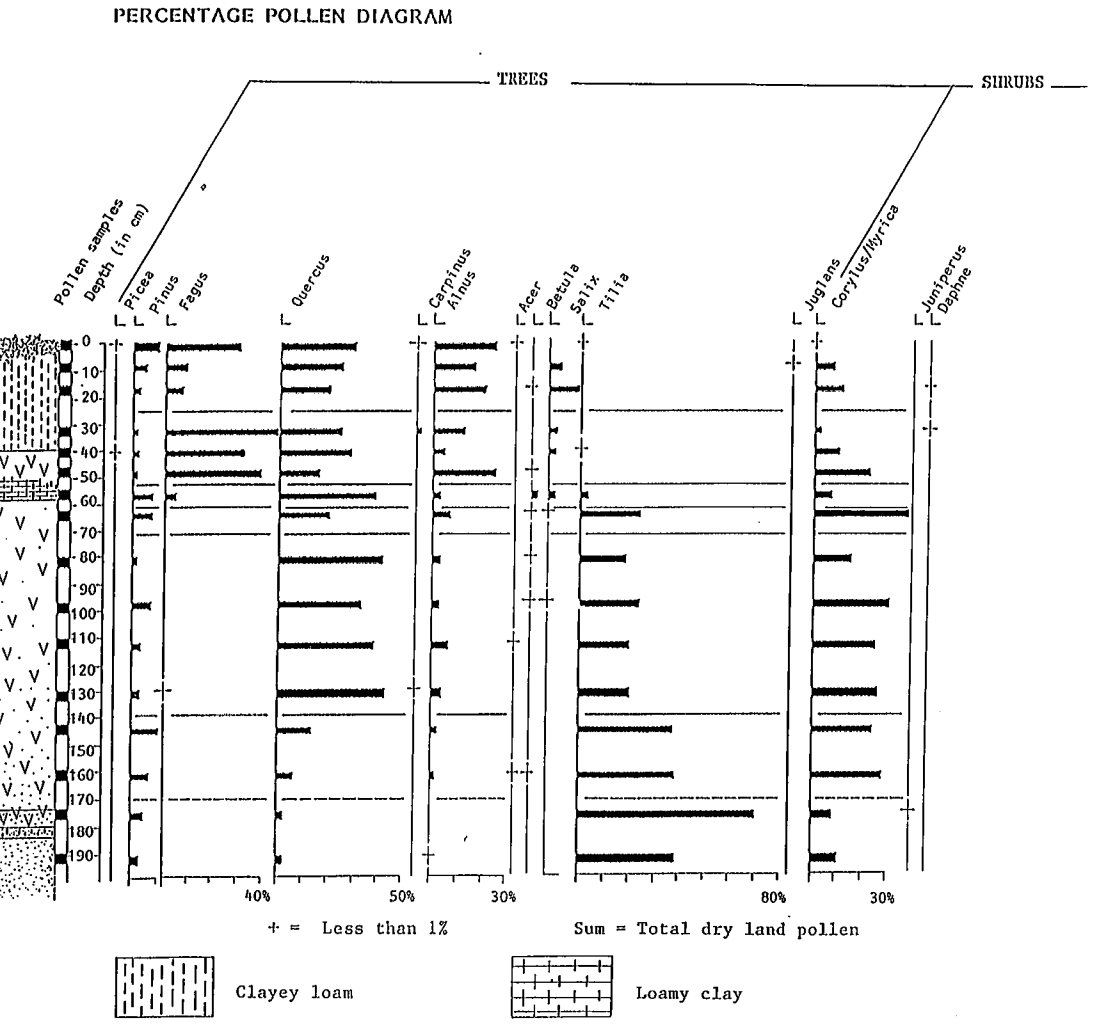
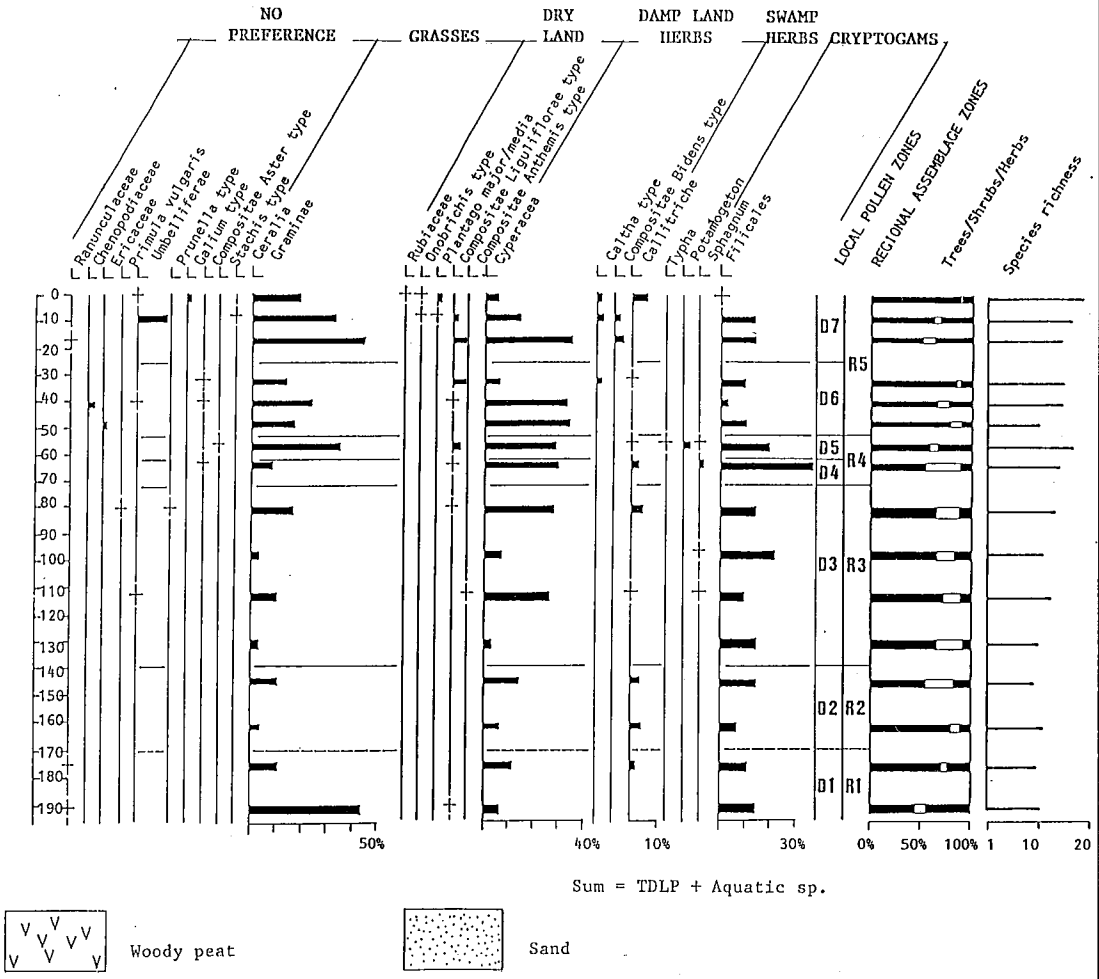


Fig. 5

To overcome the problem of interdependency of individual taxa that is intrinsic to any representation of data in percentage form (that is statistical fluctuations not related to any ecological changes) an absolute pollen diagram based on changes in the total number of pollen grains per unit volume of sediment (as estimated from the ratio of known exotic to unknown fossil pollen contents) was constructed for a selected group of major plant taxa (see fig. 6).

In the absence of radiocarbon dates, the rate of sediment accumulation could not be calculated hence the full potential of a pollen concentration diagram as a converted pollen influx diagram (mumber of pollen deposited per unit volume per year) could not be realized.



No correction factors accounting for variations in pollen production, transport, deposition or preservation were applied to the diagrams although it is clear that such factors must be considered when interpreting the results.

Unidentifiable because broken, folded, corroded or otherwise physically, chemically or biologically deteriorated grains were also counted to investigate the overall suitability of the various sediment types with respect to the preservation of pollen. Organic clays as well as peat deposits were found to possess similar amounts of damaged grains (10% to 20%). Curiously the bottom most sands did not yield higher percentages although the concentration of pollen grains was found to be much lower in the basal and uppermost samples.

The main percentage diagram shows the values of all identifiable type species. These have been split into an arboreal component including trees and shrubs and an herbaceous or non-arboreal component, comprising flowers, grasses, sedges, ferns and bryophytes. These have been further arranged according to crude habitat preferences (dry land species, damp land species, swamp species and those with broad ecological amplitude, not indicating a clear habitat preference) so as to make evident major ecological groupings at a glance.

On the left of the diagram the known values for trees and shrubs are represented as bar histograms to indicate that intermediate levels may not be inferred from a continuous line (as on many conventional pollen diagrams) while herbaceous and other pollen types are shown on the right.

A summary chart displaying graphically the way in which the total pollen sum is divided into tree, shrub and herbaceous groupings has also been incorporated just as variations in overall species richness.

On the absolute pollen diagram the estimated total pollen concentration for each level are indicated at the bottom. Values on this diagram have been joined by a continuous line in order to improve the visual clarity on the graphical display and make changes in the composition of forest communities easier to apprehend.

2.2.2. Zonation of the pollen diagram

Introduction

It would have been most obvious to use one of the existing pollen-floristic zonation schemes for subdividing the diagram into pollen stratigraphic units. Most generally applied to french, belgian and german diagrams is the Blytt/Sernander vegetation-climate periodization of the Postglacial (Pre-Boreal, Boreal, Atlantic, Sub-Boreal, Sub-Atlantic. Other inter-regional based zonation schemes such as those established by Godwin (1975) for the British Isles and by Firbas (1949) for Northern and Central Europe, met with equal difficulties in that a deductive approach involving the zonation of a site on the basis of a simplified uniformitarian scheme of inter-regional scope may not apply to local pollen stratigraphic variations and may have no climatic connotation. For this reason, a more inductive approach was adopted and local pollen assemblage zones based upon the presence, absence or abundance of one or more terrestrial pollen taxa were established by visual inspection and statistical analysis.

Thereafter, perceived similarities noticed upon comparisms with formerly published diagrams from within the study area were used to interpret the findings in the context of regional pollen assemblage zones and as a relative dating method of the observed vegetational changes.

Statistical analysis

To overcome the subjective element involved in the boundary location of biostratigraphic units (reference to previous experience, preconceptions

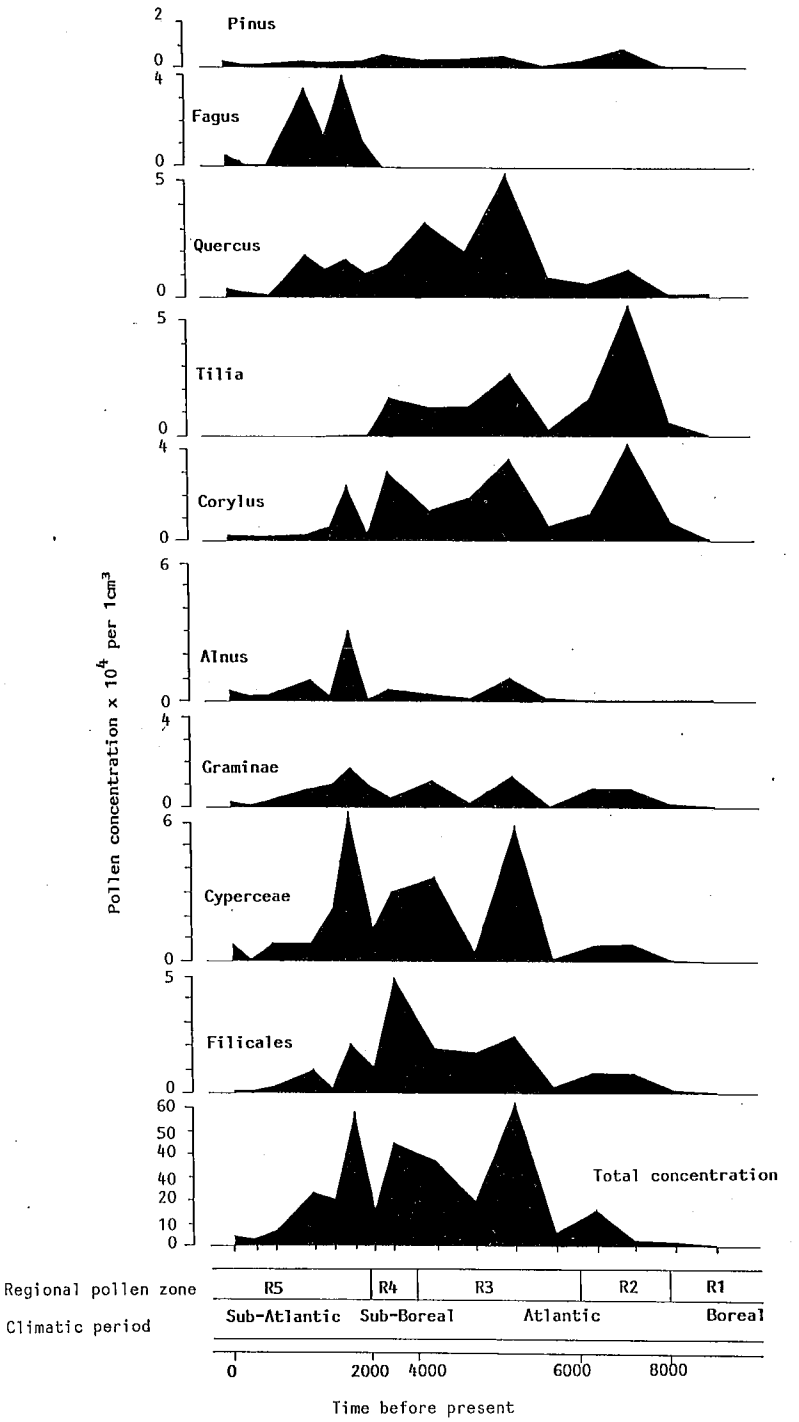


Fig. 6 Pollen concentration diagram of selected taxa

about the relevance or irrelevance of certain taxa, of time periods, of climate etc...) a type of multivariate statistical analysis which has become widely used in ecology and known as Reciprocal Averaging (Hill 1973) or Correspondence Analysis (Benzecri 1973) was applied to the percentage values of a selection of 11, mainly arboreal pollen types *(Quercus, Carpinus, Fagus, Betula, Alnus, Tilia, Pinus, Corylus, Plantago, Cerealia* and the arboreal pollen sum).

The method which is described elsewhere (Greigh-Smith 1983, Greenacre 1984, Kershaw & Looney 1985, Gauch 1982, Jongman et al. 1987) uses an algorithm that enables to ordinate (eg classify) sediments samples and species simultaneously, placing samples of similar floral composition and species of similar stratigraphic distribution adjacent to each other on a final 2- or 3-dimensional graphic output (see fig. 7). Calculations are very tedious, hence time consuming and require adequate computer software and hardware facilities.

The exact boundary location is not 'imposed' by the numerical technique and this decision is left to the investigator who has to derive it upon visual inspection of the graphical display. When the change between pollen assemblages is important, then well defined clusters enable to delimit such boundaries between similar layers with reasonable confidence. On the other hand, a more or less gradual transition or a densely packed 'cloud' of points will render arbitrary any attempt to seek further subdivisions of the data set.

In view of this problem, the objectivity of the method, as indeed that of any other multivariate ordination method, should not be overestimated and be taken for what it really is, namely an exploratory device useful to assist in the investigation of large and complex data masses in a rapid an repeatable way by reducing the dimensionality of the original data set to a few comprehensible dimensions. The interpretation of the results remains a matter of ecological insight and as anything else, it will improve with experience. Zonations obtained using this method coincided fairly well, although not perfectly, with those that would have been established by visual inspection.

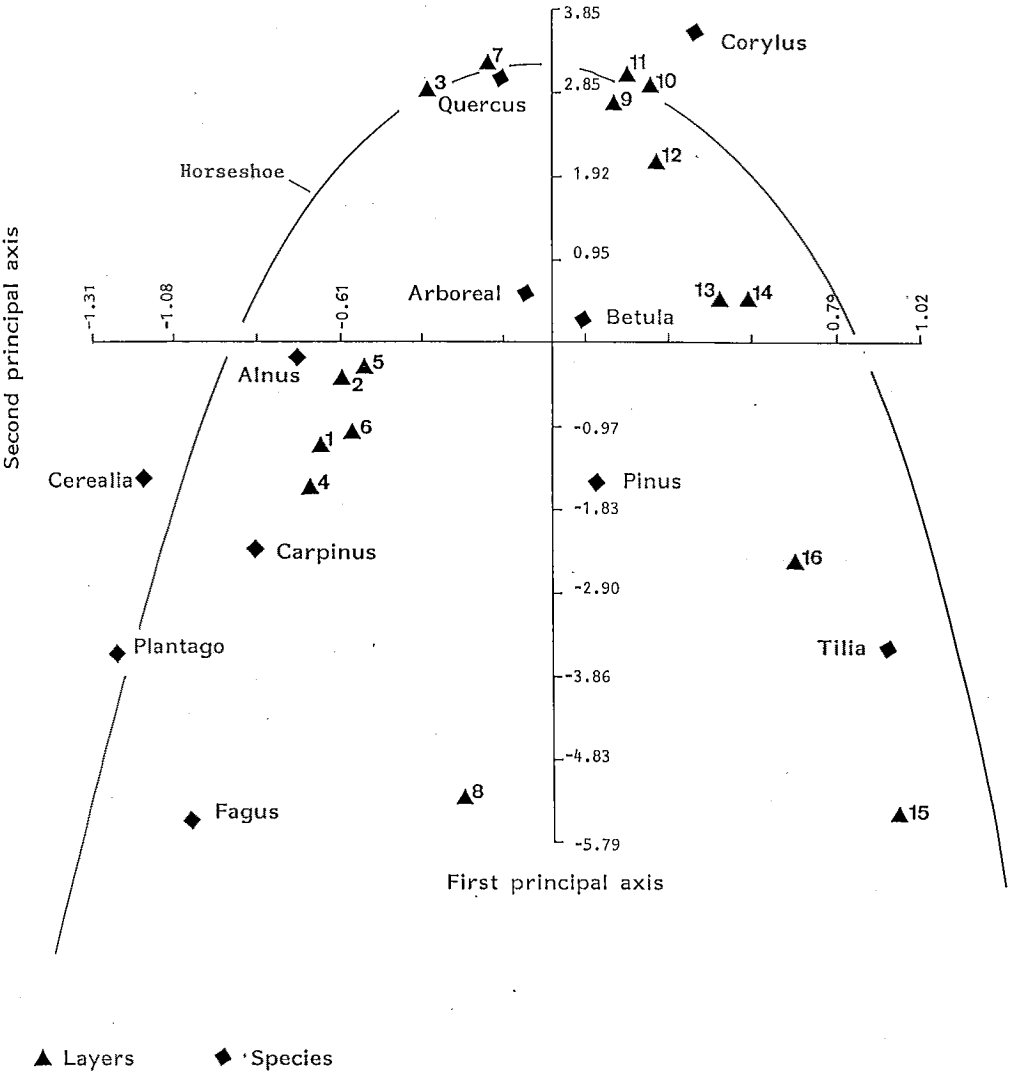
However, the effectiveness of the method for dealing with pollen data was unquestionable, so that it could be used as a good independent alternative way for identifying pollen assemblage zones on the basis of similarities and differences. The full potential of C.A. for the numerical analysis of palynological data could not be tested in detail as this would have been beyond the scope of this paper, but the application of numerical techniques in the field of quaternary palaeoecology is becoming of increasing importance (Gordon & Birks 1972).

Analysis of the data set suggested dividing the pollen sequence into 7 clusters. On one side of the plot one finds a spectra typical of the Sub-Atlantic period, with species such as beech, oak, plantain and cereals whereas on the other side, samples associated with lime, pine, hazel, birch and oak are more characteristic of the Atlantic.

The bending of the positions of objects, describing a parabolic-shaped curve is a mathematical artifact, corresponding to no real structure in the

CORRESPONDENCE ANALYSIS PLOT OF SELECTED POLLEN DATA

Fig. 7



data. A modified algorithm performing the reciprocal averaging known as Detrended Correspondence Analysis that straighten outs the 'horseshoe' has been developed by Hill & Gauch (1980). However, the author believes that there is no reason to interprete the positions of points along an arched curve rather than on a straight line. Especially when the curved pattern of points describes an environmental gradient or as here, a long term historical process documenting the evolution of a lime dominated to an oak dominated and finally a beech dominated woodland community.

2.2.3. Local pollen assemblage zone

The following local pollen assemblage zones have been established on the basis of the statistical analysis described above. Since the number of species was limited to those believed to be of regional interest, it follows that refined subdivisions based upon the occurrences of local wetland or other indicator species was not possible. On second thoughts, the author believes that indeed more types should have been taken into account. Despite this restriction however, boundary location as indicated by C.A. did not significantly differ from those that would have been established through simple visual inspection of the pollen spectra. Moreover, less rather than more assemblage zones are likely to have been retained had this been done by traditional means.

Zone DW1

The basal zone at this site is characterized by very low pollen concentrations (15000 against a site average of 204000). Of the arboreal taxa, *Tilia* is by far the most common, reaching a peak percentage of 71%. *Pinus* and *Quercus* only contribute moderate amounts upto 4% and 3% respectively. *Alnus* is present only in the lower most sample while *Corylus* consistently reaches values around 11%. *Juniper* pollen was recorded on two occasions from the upper most sample of this assemblage zone. Graminae percentages are initially very high (45%) but later drop to 11% while Cyperceae values slightly increase from 6% to 11 %. Very little dry herb pollen is found although spores of Filicales are plentiful (13%).

Zone DW2

Pollen concentration of all taxa are in net progress, reaching maximal values towards the lower boundary (326000) then slightly decreasing again (150000). Of the trees, *Tilia* and *Pinus* now reach higher percentages than earlier (14% and 9% respectively). Other arboreal pollen includes that of *Alnus* (2%) the curve of which becomes continuous and minimal amounts of *Betula* and *Acer*. The lower most sample shows a marked increase in the representation of *Corylus* (29%) also noticeable on the absolute pollen diagram. Graminae, Cyperceae and Filicales are abundant (all around 10%) while dry land herb pollen remains scarce. Of the swamp herbs, *Callitriche* is consistently present in small amounts.

Zone DW3

Total pollen concentration remains fairly high throughout the zone, being highest towards the lower boundary (site maximum of 560000). *Quercus* (33% and 43%) now dominates the arboreal spectra at the expense of *Tilia* which nevertheless remains abundant (20%). *Pinus* is still present in low amounts with values fluctuating around 5%. Of the remaining trees, stray pollen of *Carpinus, Betula* and *Fagus* could be identified. *Corylus* values are still high (up to 31%) and peak towards the middle of the pollen diagram before decreasing markedly at the top (16%). Of the local trees, *Alnus* has become more abundant, now contributing up to 7%, while *Salix* is only sparsely documented. Graminae and Cyperceae values are variable, showing two distinct peaks at the middle and top of the zone. Filicales spores are plentiful and several wet and dry land species appear for the first time.

Zone DW4

Quercus decreases quite notably to 19% while *Tilia* slightly expands to 24%. *Pinus* also shows a modest rise in percentage values, now reaching 7%. *Corylus* appears as the dominant plant species with a percentage exceeding 40%. With 7%, *Alnus* is better represented than ever before, while *Salix* remains below 1%. The curve of the Graminae drops to 8%. Cyperceae pollen is still plentiful (29%) and Filicales spores reach a maximum of 47% at this level. Little herb pollen was found.

Zone DW5

This zone is characterized by the appearance of *Fagus* (4%), the curve of which becomes continuous at this stage and the drastic decrease of *Tilia* to below 4%. *Quercus* is the most important arboreal taxa (38%) followed by *Pinus* (7%). *Betula* is present in moderate amounts (3%). Graminae have risen to 34% while Cyperceae pollen remains unchanged at about 28%. Filicales spores have fallen to 20%. A range of damp land and swamp herbs are present on the site.

Zone DW6

Fagus (32% to 47%) has become the dominant tree component with *Quercus* only arriving in second position (16% to 28%). *Tilia* has virtually disappeared from the pollen spectra and *Pinus* is found in lower concentrations than previously. Very little *Betula* and *Carpinus* pollen occurs (below 1%) while *Alnus* has become much more abundant (up to 24%), the percentage bars being depressed in mid zone (5%). *Salix* is still found in small amounts (3%). Pollen of Graminae is well represented throughout (up to 23%) whereas the Cyperceae fall to 6% after an initial peak of 34%. Aquatic or wetland species are more scarce but a wider range of herb pollen is present of which the Compositae Liguliflorae type is the most common (6%). Filicales follow a pattern similar to that observed for alder with percentage and absolute counts being higher towards the boundaries (10%) than in the centre (4%).

Zone DW7

The uppermost zone at this site. Total pollen concentration decreases upwards although all major arboreal taxa with the exception of *Salix,* follow an increasing trend on both types of diagram. Initially *Quercus* is the dominant tree pollen (25%) with *Fagus* occurring in lower quantities (9%). However, towards the top of the zone both species are found to contribute equally to the pollen spectra (30%). The values for *Pinus* are higher than ever before, reaching a maximum of 11%. Although *Salix* is fairly well represented at the base (12%) its values decrease in the middle (5%) and the species then becomes absent in the top of this zone. *Picea, Juglans* and *Daphne* pollen are found for the very first time and just like *Tilia, Carpinus* and *Acer,* they occur in very small quantity.

Corylus is poorly represented, decreasing progressively from 10% to minimal amounts towards the upper boundary. Graminae and Cyperceae are generally well documented and reach higher values at the base (45%) and at the top of the zone (19%). Among herb pollen the dry land component is particularly noticeable with type species of Cerealia, Rubiaceae and *Plantago.*

2.2.4. Regional pollen assemblage zones

Comparable local pollen assemblage zones from seven localities within the study area have been correlated and integrated into a series of distinct regional asssemblage zones.

Most pollen analytical work in the hilly eastern part of the country was carried out during the 1950's and 1960's at a time, when researchers were mainly interested in documenting major vegetational and climatic changes and not so much in interpreting their findings in an ecological context or looking for local and regional discrepancies in the vegetational history. In effet, the zonation schemes of many 'early' pollen diagrams resembled an "exercice in fitting the data from the site under investigation into a predetermined mould" (eg Godwin or Firbas pollen zones or Blytt-Sernander climatic episodes) (Moore & Webb 1983). These authors also point out that the significance of many local and to a lesser extent regional variations, has been lost as a result of this concern for conformity.

The development of major plant communities following the last ice age has been well evidenced across Europe and one may ask whether there is anything left to explore. The answer is yes. In the words of Grosvenor (1988) "There's a whole world yet to be discovered, not of mysterious places but of relationships among the places". Thirty years ago, 'great explorers' were busy filling in the blanks of vegetational development. "What we haven't filled in yet are the blanks of knowledge about the causes of these events and how they all fit together - an even greater challenge that requires a new kind of exploration".

The 'european' concept of quaternary pollen zones as a biological, climatic, temporal division in the history of a flora is of little ecological value and should be supplanted by the more appropriate 'american' view that

defines a zone purely upon its microfossil content which need have no existence outside the locality in which it is recognized (Cushing 1967). The implication of this is that each pollen diagram can be zoned independently upon its own features without reference to any other pollen diagram. Consequently, a pollen assemblage zone such as those described above, may simply refer to a state of the local vegetation at a particular moment in time and indicate successional developments or small scale natural or anthropogenic patterns.

More often one is concerned with extra-local (inter-regional or intra-regional) changes in which case the pollen types which are known to be of local origin (generally wetland or aquatic species) can be ignored when constructing a regional zonation scheme. As a result, this treatment will reveal developments that are expected to show-up in other diagrams of the region. Such regional pollen assemblage zones are named after the most conspicuous pollen components rather than being numbered and may be used as a relative dating method (regional assemblage zones had to be labelled on the diagrams because of space shortage!).

So far very few radiocarbon ages have been obtained in the context of published pollen analytical work in the area and periodization of the regional assemblage zones therefore had to be based on the classical Blytt-Sernander climatic episodes and Firbas pollen zones as dated by Guillet (1972) in the nearby Vosges massif by ^{14}C. No regional pollen assemblage zones have been constructed for the Late Glacial (12000 b.c - 8300 b.c.) nor the Early Lower Postglacial (83000 b.c. - 73000 b.c.) as these periods have sofar only been sparsely evidenced (Couteaux 1970).

Regional pollen assemblage zones constructed from the Later Postglacial horizons may be delimited as follows:

Pinus-Corylus assemblage zone

Type locality: Echternach, Letschen 2, phase 6, 113-109 cm, peat (Couteaux 1970).

Description: The zone is characterized by modest amounts of *Corylus* pollen with plentiful of *Pinus* and Filicales spores and little *Betula* and *Ulmus*. Graminae are abundant while arboreal pollen other than pine generally remains low.

Contacts: The lower limit is drawn at the decline of *Betula* and sharp increase in *Corylus*. The upper boundary is placed at the decrease of pine and ferns and slight increase of alder, lime and oak pollen.

Other occurrences: Loschbour, samples A11, A9, A7, A5, tufa, Gob et al. 1984.
Berdorf ?, Dauwelsmuer, zone DW1, 192-176 cm, peaty sand.

Notes: At Echternach, this zone is dominated by *Pinus* (up to 40%) while at the sites of the Loschbour and Berdorf the conifer was found to be relatively scarce (around 5%). This may be due to edaphic factors favouring the growth of pine woodland on the peat deposits of an abandoned meander of the river Sûre (causing a local over-representation) while on the steep and mineral valley slopes the tree may have been more sparsely distributed.

At Berdorf, the very high percentage values for *Tilia* (up to 71%) of the lowermost sandy horizons could reflect an over-representation of the species, this time, as a result of preferential preservation related to high sporopollenin contents of its pollen grains (Havinga 1964).

Furthermore it could be argued that pollen spectra of these bottom samples are likely to have been influenced by taphonomic processes such as infiltration and preferential migration of pollen from the organic surface deposits into the coarse mineral sediment. Also, corroded *Tilia* pollen generally remain easily identifiable whereas that of other species often may be problematic!

However, it should be no surprise to find higher values for lime on the mineral soils of the valley slopes as these correspond to the habitat requirements of the thermophilous tree. Being mainly an insect pollinated species, its relatively large and heavy pollen will consequently not be transported over great distances (Mullenders 1962, Planchais 1970) to those often large, wetland sites investigated by palynologists and generally located away from the centres of production. In view of these problems, this regional assemblage zone should not be regarded as well defined and remains tentative.

Age: Echternach and Loschbour: Lower Postglacial, Boreal period, Firbas zone V, 7300 b.c. - 6200 b.c.
Berdorf: Late Boreal.

Corylus - Tilia assemblage zone

Type locality: Berdorf, Dauwelsmuer, zone DW2, sandy peat.

Description: Dominated by high values of *Tilia* (40%) and *Corylus* (30%) with abundant *Pinus* and *Quercus* (10% and 15%). Herb pollen is scarce.

Contacts: The lower limit of the zone corresponds to the expansion of *Corylus* and slight increase of *Pinus* and *Quercus*. The upper boundary is drawn at the decrease of *Tilia* and *Pinus* to values of respectively 20% and 40% and the renewed increase of *Quercus* to over 40%.

Other occurrences: Echternach, Letschen 1, 119-100 cm, peat;
Echternach, Letschen 2, 108-90 cm, peat, Couteaux 1970.

Age: Middle Postglacial, Early Atlantic - Middle Atlantic period, Firbas zone VI, 6200 b.c. - 4000 b.c.

Corylus - Tilia-Quercus assemblage zone

Type locality: Berdorf, Dauwelsmuer, zone DW3, peat.

Description: The zone is dominated by *Quercus* (30-40%) with high amounts of *Corylus* (25%-30%) and *Tilia* (20%-25%). *Pinus* is found in small quantities (5%). *Ulmus* is scarce.

Contacts: The lower limit is drawn at the expansion of *Quercus* while the upper boundary was placed at the marked decrease of the same taxa and increase of *Corylus* pollen and Filicales spores.

Other occurrences: Echternach, Letschen 1, phase 8, 105-100 cm, peat;
Echternach, Letschen 2, phase 8, 95-90 cm, peat (Couteaux 1970)
Reisdorf, Bigelbaach, Haard 4, 50-44 cm, peaty sand (Couteaux 1969).

Age: Middle Postglacial, Middle Atlantic - Early Sub-Boreal, Firbas zones VII and VIII, 4000 b.c. - 2200 b.c.

Corylus-Tilia-Quercus-Fagus assemblage zone

Type locality: Reisdorf, Bigelbaach, Haard 1, 40-22 cm, sandy peat (Couteaux 1969)

Description: *Quercus* is the dominant arboreal taxa but together with *Corylus* and *Tilia* follows a decreasing trend throughout the zone. The latter species almost disappears from the pollen record towards the top. *Fagus* appears for the first time in moderate amounts in mid-zone and then sharply increases to values of over 20%. *Betula* and *Pinus* pollen are slightly more abundant but remain relatively low.

Contacts: The lower boundary was drawn at the onset of the decrease in *Quercus, Corylus* and *Tilia* values whereas the upper boundary was placed at the vanishment of *Tilia* from the pollen spectra and an overall decrease of the arboreal component.

Other occurrences: Reisdorf, Bigelbaach 3, 22-20 cm, peaty sand;
Reisdorf, Bigelbaach 4, 32-28 cm, peaty sand;
Reisdorf, Bigelbaach 5, 30 cm, peaty sand;
Reisdorf, Bigelbaach 6, 34-30 cm, peaty sand (Couteaux 1969)
Echternach, Letschen 1, phase 9, 97-90 cm, peat;
Echternach, Letschen 2, phase 9, 88-84 cm, peat (Couteaux 1970);
Berdorf, Dauwelsmuer, zone DW4 and DW5, peat.

Age: Upper Postglacial, Sub-Boreal - Sub-Atlantic period, Firbas zone IX, 2200 b.c. - 250 b.c.

Quercus - Fagus assemblage zone

Type locality: Beaufort, Birkbaach 1, 101-0 cm, peat (Couteaux 1969).

Description: This assemblage zone is dominated by *Fagus* and *Quercus,* the former appearing to be slightly more abundant. *Corylus* progressively decreases throughout the zone. *Carpinus* is found in small amounts and a range of dry and open land pollen is present notably *Rumex, Plantago* and *Cerealia. Picea* and *Pinus* become more frequent towards the uppermost horizons and *Juglans* pollen may occur sporadically.

Contacts: The lower boundary is placed at the beginning of continuously high *Fagus* values and a more pronounced decrease of *Corylus.* This is the uppermost regional pollen assemblage zone and the upper limit therefore corresponds to the present day surface.

Other occurrences: Beaufort, Birkbaach 1, 10-0 cm, peat (Sauvage 1951);
Beaufort, Birkbaach 2, 90-0 cm, peat (Sauvage 1951);
Beaufort, Birkbaach 3, 125-0 cm, peat (Sauvage 1951);
Beaufort, Birkbaach 4, 100-0 cm, peat (Slotboom 1963);
Altrier, 110-0 cm, peat (Slotboom 1963);
Reisdorf, Bigelbaach, Haard 1, 20-0 cm, sandy peat;
Reisdorf, Bigelbaach, Haard 2, 34-0 cm, sandy peat;
Reisdorf, Bigelbaach, Haard 3, 18-0 cm, sandy peat;
Reisdorf, Bigelbaach, Haard 4, 21-0 cm, sandy peat;
Reisdorf, Bigelbaach, Haard 5, 28-0 cm, sandy peat;
Reisdorf, Bigelbaach, Haard 6, 28-6 cm, sandy peat (Couteaux 1969);
Echternach, Letschen 1, 87-85 cm, peat;
Echternach, Letschen 2, 83-87 cm, peat (Couteaux 1970);

Berdorf, Aesbaach 2, 64-58 cm, peat (Couteaux 1970);
Berdorf, Dauwelsmuer, zone DW6 and DW7, peat;
Berdorf, Huuscht (Schwenninger, unpublished);
Berdorf, Vugelsmillen (Schwenninger, unpublished);
Berdorf, Meschelshéd (Schwenninger, unpublished);

Age: Upper Postglacial, Sub-Atlantic, Firbas zone IX, 250 b.c. - present day. A radiocarbon age of 130 b.c. ± 80 was obtained for a peat sample from Beaufort, Birkbaach: Gilot 1968, Lv 220 (Couteaux 1969).

DISCUSSION

3.1. Sedimentation and local vegetational history

The small, steep sided basin may have formed as a result of slope failure such as landslides along a well defined shear plane. The unusual location of the waterhole on a 'broken' slope segment of the valley of the Black Ernz could be related to a type of rotational slip involving a mass movement of badly drained and overburden colluvium.

Initially the depression may have been filled rapidly with eroded sand from the adjacent hill slope. The dating of the site formation processes remains uncertain although the presence of high concentrations of ash or soot particles within the pollen slide preparations of the lowermost sands could point to evidence for volcanic activity in the nearby Eifel (Germany). Radiocarbon dates of the latest volcanic eruptions indicate an age between 9000 b.c. and 8000 b.c. (Hary 1966).

Under the increasing influence of tropical air masses during the Late Lower Postglacial (7300 b.c. - 6200 b.c), higher precipitation levels and 'optimal' growing conditions for plants may have favoured natural silting that caused the site to become waterlogged and enabled the onset of peat accumulation. During the Middle Postglacial (Atlantic period, 6200 b.c. -3200 b.c.) sedges and ferns colonized the fringes of the depression and pollen of several damp land and swamp herbs point to the persistence of open water until zone DW6.

The stratigraphy of the higher levels suggests a rapid shallowing of the water level. This is a frequent hydroseral stage for this type of small water body where the development of a fringing reed swamp and/or the proximity of broadleaved woody species (hazel, oak and lime, hence a woody peat!) considerably speed-up the natural silting process. The absence of pollen of submerged or floating leaved macrophytes from zones DW1 to DW4 suggests that water depth may have been too great to allow the establishement of much aquatic vegetation across the site or that they may have been quite scarce and more pollen would have had to be counted in order to detect them. Consistent low amounts of sand grains found within the peat deposit may indicate the throughflow of drainage or seepage water from the hillslope.

During zone DW5, roughly corresponding to the Sub-Boreal (warm and dry climate), a thin detrital clay developed at the deepest western part of the site and the finding of *Typha* and *Potamogeton* pollen points to favourable

conditions for aquatic species. Cyperceae and Filicales continue to be important components of the bog community.

In the succeding woody peat horizon of the Sub-Atlantic (cold and wet climate), open water species have disappeared again while high values of *Alnus* and *Salix* give evidence of the development of an alder-willow carr at a short distance from the coring locality. Peat formation ceased during zone DW6 probably in response to a shallowing of the water, combined perhaps with occasional phases of dryness. Profile features such as mottling that results from the oxidation of iron were found in the better aerated clays of zones DW6 and DW7 and support the idea of a seasonnally fluctuating watertable further responsible for higher rates of organic decomposition and pollen corrosion.

As a result of natural silting, the flooded surface of the basin increased and for most of the Upper Postglacial (Sub-Atlantic, 250 b.c. - present) local site conditions have favoured the growth of *Alnus* which has become the most important taxa of the local marsh vegetation. Initially, pollen may have originated from a belt of trees surrounding the basin although presently the tree is about to invade all of the site. Truly aquatic species are lacking and this may be due to brackish water conditions. Lower damp land pollen values further reflect the increasing terrestrial status of the carr taht may soon become overgrown by deciduous broadleaved trees.

3.2. Regional vegetational history

3.2.1. Late Lower Postglacial forests

During the Late Lower Postglacial (7500 b.c. - 6200 b.c.) the *Pinus-Corylus* regional pollen assemblage zone reflects the development of a pine woodland across the peat bog of the alluvial plain at Echternach. Pollen productivity of this wind pollinated conifer is extremely high and the tree is likely to be overrepresented in the pollen diagram. The woodland appears to have been open enough to support a range of light demanding species notably *Corylus.* The abundance of the latter suggests that it may have flowered profusely as a canopy tree rather than as an undershrub.

Of the other trees present, *Betula* and *Ulmus* appear to be the most common ones initially, although the appearance of thermophilous taxa such as *Quercus, Tilia* and *Alnus* provide evidence for a more diversified forest community than it may at first be assumed. At an early stage hazel may have grown in patches devoided of a dense tree cover as well as spreading out into the pine woodland whereas later it may have become largely reduced to an understorey shrub.

In the absence of further comparative spectra from sites of contrasting geographic location, it cannot be said whether the vegetation remained relatively homogenous over a wide area or if distinct patches of plant communities already developed in parts of the region. The model of vegetational development proposed here should therefore be taken with care and must be considered as a first attempt to outline the spatial distribution,

structural as well as compositional changes undergone by the major tree population.

Pinus which has broad ecological amplitude and shows great adaptability to different environments, may have been preponderant more or less everywhere, whether in dry or wet habitat situations of the valley bottoms, slopes or the plateaux. Being a common tree scattered across the landscape it comes of no surprise that analyses of charcoal remains from a meolithic rock-shelter site at Berdorf revealed the conifer to have been a major source of firewood (Leesch 1983).

On the valley slopes, pine stands are unlikely to have been densely packed, leaving plenty of space and light for herbaceous ground cover species, birch and hazel. Due to the open structure of the canopy, pollen and fruit production of the latter are likely to have been abundant and the collecting of hazel-nuts may have been an important seasonal food gathering activity among contemporous hunter-gatherer communities. The arrival of thermophilous taxa may at first have been more pronounced in the bottom lands of the deeply incised valleys where communities capable of withstanding periodic inundation of their root system *(Alnus, Salix)* may have displaced or at least, compete effectively with pine and birch on the river flood plains (hence little pine pollen during the Boreal at the Loschbour). Oak and lime may also have grown intermittently within such deciduous lowland 'gallery' forests as early as the mid-Boreal. From such initially restricted ranges they could have expanded up the altitudinal gradient as climatic conditions became more favourable to their establishement.

The prevailing regional climate is the most obvious controlling factor for the structure of terrestrial ecosystems and is commonly evoked in pollen analytical works. But certain other factors are equally significant at least, in areas affected by certain non-climatic phenomena such as constrasting landforms, natural and anthropogenic disturbances that mold microclimates and micrhabitats and which should deserve attention. Characteristics of landforms may include aspects such as relief, flatlands or slopes and plant as well as animal communities are expected to change accordingly. The implications of such non-climatic environmental factors are important and such elements must be taken in account for understanding and reconstructing past patterns of plant communities.

Slopes are significant and variable subunits of a landscape that are commonly affected by erosion, the rate of which is related to its steepness, soil type and vegetation. Steep slopes such as those encountered on the river valleys of the Black Ernz or Sûre are more susceptible to instability and fewer plants can survive on steep slopes than in other environments. Those that can, need extensive root systems to anchor themselves against landslides or eroding soil.

During the last glaciation, the harshness of the environment implied a reduced vegetation cover and consequently soil creep and slope wash are likely to have been highly active on hillslopes, thereby causing a thinning of soils and leaching from the upper to the lower slopes which therefore would be enriched in nutrients. Potential erosion may have been greater than the

weathering rate and because weathered debris (free fall of fragments from the cliff face) will be transported away before a soil can form, the slopes of the major river valleys may to a great extent have been 'weathering limited' (Trudgill 1983) until the Boreal period. This is in contrast to the present day 'transport-limited' slopes, where the soil cover gets thicker with time.

The aspect of a slope or the direction in which it deeps can have profound effects on the microenvironment. North facing slopes in north temperate latitudes experience reduced solar radiation and if the slope is steep enough it may never or receive very little direct sunlight at all and because such slopes are cooler than others, they may be covered by a correspondingly 'cooler' climate community than that covering a south or even west facing slope.

Taking into account these factors it may therefore be suggested that pine, birch and hazel are likely to have dominated the Borel pollen spectra not so much because prevailing climatic conditions (believed to be generally warm and dry) would have inhibited the growth of thermophilous species but because former pioneer species may have benefitted from favourable edaphic and micro-climatic conditions that confered them a competitive advantage until the end of the period on these common and largely denudated and disturbed slope grounds. Oak, lime, elm and alder may already have been present in the area in small quantities either as sporadic individual trees or as larger family clusters confined to specific localities and 'waiting' to expand their range with ongoing successional processes and not, as generally assumed, climatic change.

Alternatively, one could put forward the idea of a large scale and repetitive natural disturbance factor inhibiting the establishement of broadleaved woody species thereby maintaining an early seral type of community comprising mainly pioneer plants as noticeable from the pollen record (hazel, birch, pine, graminae).

Fire is an all to often underestimated feature of natural ecosystems. Any habitat that is occasionally dry enough to create a fire hazard, but normally wet enough to produce and accumulate a thick layer of inflammable plant detritus as this may have been the case during summers in the Boreal, is likely to be influenced by fire. Many communities at least in the temperate zone have developed in concert with natural fires although these are presently only generally recognized in Northern Europe as a major hazard during exceptional droughts (eg 1976!).

Seasonal or periodic light fires apply selective pressure that favour the survival and growth of some species at the expense of others. Given enough time, natural communities evolve that may be described as 'fire types' and their prosperity or very survival will depend on fire. Forests perpetuated by fire include fire resistant species that may have a very thick bark (at least in the lower stem areas as in pine), protected growing portions by burial in the ground (as for hazel and grasses) or reproductive organs that do not release their seeds until burned (serotinous pine cones) or produce large quantities of widely dispersable seeds (as for birch and many r-selected individuals), that allow rapid and opportunistic recolonization of open grounds.

Fires destroy above ground biomass while leaving root tissues relatively untouched and fire adapted plants store biomass in roots where it is protected from light fires by the soil, whereas aboveground parts of many ground flora species notably grasses but also shrubs such as hazel, may regenerate by stem sprouting or from growing points hidden below the soil surface.

Fire is even necessary to the life history of some pine species that do not shed seeds unless triggered by the heat of a fire passing through the understorey below. The vast southern pine forests in the Gulf coast of the U.S.A. are maintained by periodic fires. The pines are better adapted to withstand scorching under conditions that destroy oaks and other broad leaved species (Ricklefs 1979). After a fire, pine seedlings enclosed in cones may become destroyed but beside those opening at maturity, others are serotinous (resin coated) and open only when heated - an insurance policy to release new seed immediately after a fire. Seedlings will grow rapidly in the absence of competition from other understorey species (Cooper 1961, Kozlowski & Ahlgren 1974).

Natural fires set by lightening have characterized the redwood forests of the Sierra Nevada and chaparral vegetation (a fire type shrub) as well as North-American lodgepole pine woods are seral, their survival depends on fire otherwise they are succeeded by shade tolerant understorey species.

Could it be that in the 8 and 7 millenia b.c. the stipulated pine-hazel-birch forests of valley slopes in eastern Luxembourg formed a fire maintained climax community? A type of woodland almost programmed for periodic destruction by fire?

As the community matures, accumulated litter and dry wood become so dry that fungi and bacteria cannot act on the lignin so that inflammable materials may have pilled up faster than they could be decomposed during the long dry summer months. As the community becomes more and more susceptible to combustion, fire sooner or later sweeps through the woodland, removing detritus and killing shrubs and understorey trees back down to ground level. A successional phenomena that repeats itself as the woody vegetation resprouts and grows to maturity again.

At present such a challenging and somewhat extravagant hypothesis may lack sound evidence but at least it offers the advantage to combine present day observations and knowledge of plant community ecology with historical findings about the prevailing climatic conditions as derived from oxygen isotope analysis of deep-sea cores (warm and dry), the vegetation as reflected in pollen and charcoal spectra (mainly pine and hazel with little oak), the occurrence of ash or soot particles in pollen preparations and the phenomena of red coloured oxidization patches to be found in remote parts of sandstone boulders and cliff faces within the study area and commonly believed to be caused by fire.

One may also take the idea a step further and wonder whether such a phenomena could have had any implications on the behaviour of animals as well as man.

Woody debris on the forest floor contains considerable amounts of nutrient minerals that would be released for recycling very slowly through decomposition. Fire releases them to the environment virtually immediately and it may be seen as actually increasing productivity by speeding-up recycling. Certainly the big game herds of Africa or the deer in California chapparral or elk in the Yellowstone National Park do not thrive unless periodic fires bring on a flush of new palatable foliage.

Burning has been shown to improve both the quantity and quality of browse for ungulates (Dills 1970) by reducing the height of the existing browse, bringing it more within reach of smaller ungulates and by facilitating the establishement of more browse plants in the disturbed patch. Flower and fruit production varies greatly with habitat and the allocation of net production to flowers and fruit is highest in grasslands, intermediate in shrubby habitats and lowest in forests whereas the allocation of production to roots and stems follows an increasing trend. In other words, fire disturbed habitats would yield a diverse and abundant source of plant foods (foliage, fruits) for man and animals to feed upon (plenty of berries and hazel nuts). The proportion of above ground biomass in leaves is also higher in grasslands and young forests than in mature forests (Ricklef 1979). Leaves comprise between 1% - 10% of aboveground biomass of forests, 20% to 60% in shrubs and is a larger proportion in shrubby habitats than in the shrub layers of forests. This shows that the allocation of net production by plants is more suitable and available to herbivores in open grassland or shrubland than in forests.

Fire clearance gaps may have considerable ecological effects among which the boosting of plant and animal productivity and species diversity during secondary succession may be the most important ones. Wild grazers and browsers such as deer and aurochs are likely to be attracted to such glades and the carrying capacity of their populations or the physical condition or fitness of individual animals may be increased. Structural changes in canopy architecture may have been favourable to other species such as wild pig, hare and game birds that may have benefitted of a dense shrub vegetation as a feeding patch but also as an ennemy escape to avoid being preyed upon by predators such as wolves, bears and lynx.

Wild animals were a major subsistence resource to humans and several mesolithic exploitation camps from which hunting of large mammals for meat and fur was carried out have been found by archaeologists working in an area, that appears to have been a favoured seasonal hunting ground for aboriginal populations for several millenia (Gob et al. 1984, Blouet et al. 1986).

Finally, the pertinent question to ask is whether fire could have been used as a manipulative tool by human communities to influence the game populations so as to increase their numbers, body weights and distribution as well as the chances of killing them?

Certainly the use of fire as a tool for managing natural resources is a well known technique applied to National Parks in America, Africa and Australia and similar evidence from ethnographic studies is also well documented. With respect to the archaelogical record, Simmons (1975) rightly points out

that he "economy of mesolithic folk has always been assumed to be of the food collecting rather than food-producing type and to have had an emphasis on hunting and gathering" while on the other hand, evidence for agriculture (cereal and weed pollen) is found almost exclusively in a distinct neolithic context. This traditional two-fold division has left one further mode of subsistence all too often unconsidered, namely that of herding.

Some researchers have discussed the hypothesis of regular and recurrent burning by mesolithic hunting populations in the southern Pennine Uplands of Great Britain (Mellars 1976, Jacobi et al. 1976, Simmons 1975) and the role of pastoralism as being part of a package of indigenous developments by local populations has become of increasing interest in the debate about the origins of farming (Dennell 1982, Barker 1985, Zvelebil 1986).

Traditionally, the beginning of prehistoric farming has been explained by a process of colonisation from the Near East in response to population pressure, thereby terminating the aboriginal way of life whereas more recently, researchers have realized the complexity of the process and taken in consideration a combination of local and intrusive developments.

Here it is suggested that natural fires affecting commonly the Boreal pine-hazel forest of the study area may later have become of anthropogenic origin following the realization of increasing benefit to be taken from such disturbed patches of vegetation by contemporaneous mesolithic folk. These may have experienced a sequence of cultural changes as they evolved from a preponderantly hunting and gathering way of life to a pastoral mode of subsistence that by its transitional nature, may have facilitated the development in due time of first agricultural communities and later industrial societies.

3.2.2. Middle Postglacial forests

The opening of the Atlantic period (5500 b.c. - 3000 b.c.) typically reflects an increase in percentage values of alder. Presumably, the tree benefits of the more favourable wet and mild climatic conditions attributed to this period. *Quercus* and *Tilia* rapidly become established as the major arboreal components at the expense of pine and birch, whereas *Corylus* appears to grow well as an understorey shrub in a relatively open and illuminated woodland.

Under the increasing influence of tropical air masses, a weakening of the continental climatic regime and higher precipitation levels may be expected and as a consequence, fires may have become less frequent while deeper slope soils may have enabled the establishement of broadleaved woody species which successfully outcompeted the existing pioneer community.

In the light of previous pollen analytical work, the abundance and dominance of *Tilia* in the Atlantic spectra of the site studied here is unexpected and deserves special attention. The diagram shows relatively high percentages of *Tilia* (average 30%-35%) notably in the earlier phase (up to 70%). If one takes in account the fact that this entomophilous (insect pollinated) species produces less (although still abundant) pollen than wind pollinated species such as pine, alder, hazel and oak (Pohl 1937), one may claim with

confidence that if the data were calculated using correction factors, lime would be even more predominant than this may appear on the pollen diagram. In Denmark, lime is now recognized to have been the commonest tree in the forests of the Atlantic period while in our latitudes, the tree generally only bulks much larger than in any later period (Andersen 1973).

Woods dominated by lime are presently found in places where the growth of beech is limited either by natural or human factors. In many respects its distribution is similar to that of hornbeam (Ellenberg 1987). However the tree has higher light demands than the latter and is therefore often found on soils which are nutrient poor and do not enable optimal growth of other trees. The somewhat delayed appearance and expansion of *Tilia* as compared to *Quercus* during the Postglacial warming-up can be interpreted in terms of the present day northern distribution of both species. *Quercus* extends further into Scandinavia than *Tilia* (Becker 1983) and may therefore be expected to have recolonized periglacial regions prior to lime.

Extensive lime woods are nowadays only found in some parts of the Soviet Union and the tree only plays a minor role in West-European forests. On the basis of this it could be argued that the expansion of *Tilia* during the Atlantic may have been linked to a more pronounced continental climate. This however, clearly was not the case until the end of the period and the type of atmospheric circulation suggested over northern Europe between 5500 b.c. and 3000 b.c. indicates a displacement of the polar front back northwards, causing a renewal of warmth and the passage of depressions (Magny 1982) which have led researchers to consider the Atlantic period as the 'climatic optimum' or hypsithermal interval of the Postglacial when mean annual temperatures were generally 2°C to 3°C higher than at the present day.

Corresponding assemblage zones from other sites show that although *Tilia* is present in almost every assemblage zone, the tree nevertheless reaches exceptionally and unequalled values at the site considered here. Lime pollen is poorly dispersed in comparison to hazel, alder, birch, oak and elm not only because of its relative large size (maladaptation to wind dispersal) but because the tree flowers when the forest is in leaf and horizontal wind velocities are low and pollen are trapped by the foliage and poorly dispersed within the trunk space. Consequently, unless the pollen core site is located close enough to the centre of production, pollen is unlikely to be transported over great distances to those sampled wetland sites that often do not correspond to the natural habitat of the species. Hence the tree is likely to be under-represented in many pollen diagrams.

With respect to the site considered here, one may therefore suggest the existence of purely local or small scale regional factors taht may have been suitable to the development of an oak-lime-hazel forest. High *Tilia* values approaching those presented here are only found in a diagram from Nothum in the Ardenens (Kwaad & Mücher 1976).

Interestingly, these authors obtained a pollen core from a dry bottom valley site located next to a steep slope and therefore it may be argued that the topographic location, corresponding to a specific landscape unit such as a steep slope, may have been a relevant factor in shaping the plant commun-

ity. Whereas oak may have been predominant on plateaux soils, lime could have been the commonest tree on valley slopes with hazel growing well in both types of habitat. Alder may have been the major arboreal taxa of wet bottom valleys and on isolated wetland sites. Pine and birch have been displaced from their former wide range but do not seem to have disappeared from the area. Both pioneer species are likely to have become restricted to a great extent to rocky sandstone outcrops located around plateaux margins, where they may still be found at the present day.

Thus the reason why lime appears to have played such an important role in the Atlantic pollen sequence of the region may be linked to its superior competitiveness with oak in the hillslope woodland on calcareous or base rich and relatively young shallow soils. Furthermore, the absence of a competitor with similar niche characteristics (eg *Fagus)* may also be of relevance and it may be argued that the presence of *Tilia* may just as well be related to the absence of a competitor. This could be interpreted in terms of the better seed dispersal efficiency of lime that may have enabled the tree to colonize new areas more rapidly during the Postglacial warming-up from its glacial frontline than beech. A possible explanation for this may be seen in the respective nature of the two types of seeds, former being much smaller hence lighter as well as possessing a large membraneous bracteole acting as a wing (as in the case of sycamore and pine seeds) that enables better wind dispersal of seeds, whereas nuts of beech are likely to drop closer to the parental tree and may experience severe losses due to the fact that they constitute an attractive food resource for many small mammals and birds. Climatic conditions during most of the Atlantic are likely to have been favourable to the growth of beech and may therefore be ruled out as limiting factors.

Better dispersal adaptations and seed survival rates may thus explain why during some 3000 years, lime was a major component of the forest community. The role of reproductive strategies and seed dispersal adaptations of various trees during the postglacial recolonization process would be an interesting research topic for future investigations.

3.2.3 Upper Postglacial forests.

The long term tendency of climatic development from the Atlantic to the Sub-Atlantic was one of slow deterioration involving a displacement southwards of the polar air masses and a diminishing of the beneficial influence of tropical air, causing a lowering of mean annual temperatures and increase in precipitation (Magny 1982). Shorter-term climatic fluctuations characterized by the marked influence of the continental cold and dry polar air bring about periods of improved conditions eg. hot summers and less precipitation. But from 800 b.c. onwards, northern Europe seems to become more influenced by maritime air masses (cold and wet) hence an accentuated climatic deterioration. Limbrey (1978) has suggested that the possible dry summers of the Sub-Boreal may have contributed to the eluvial horizons of argilic brown soils but implies that their initiation resulted from the activities of Neolithic cultivators.

In the Luxembourg Ardennes, mass wasting deposits are thought to have occurred during the Atlantic and/or the Sub-Boreal (Kwaad and Mücher 1977) and clay migration is believed to have taken place in a climate drier and possibly warmer than today (Langohr and Van Vliet 1979). In the pollen core the spectra corresponding to the Sub-Boreal was obtained from an argilic horizon but its origin remains uncertain. It could indicate increased erosion as a result of forest clearances and agricultural activities on the plateau, leading to sediment deposition on the valley slopes although alternatively, purely local formation processes related to a lowering of the water table and enhanced rates of decomposition of plant material may be responsible for the ceasing of peat accumulation and the development of an organic clay.

Probably both types of phenomena have acted together. Evidence for human activity in the late Atlantic and Sub-Boreal may further be suggested by a noticeable decrease in arboreal pollen concentrations on the absolute pollen diagram. Oak and lime values drop by almost 50% while pioneer species such as hazel and birch become more abundant. The impact appears to have affected the plateaux as well as the slope forests. Oak woodland which is likely to have covered the entire surface of the Berdorf plateau could have been affected by major clearances related to the establishement of an agricultural community.

Slope forests may have been affected to a lesser degree as they are not very suitable for growing crops and pulses and clearances are more likely to have affected the gentle slopes of the bottom valley. However the stipulated lime woodland on the steeper slopes may nevertheless have been adversely affected by the cutting of tree leaves for winter fodder during the Neolithic and Bronze Age. Leaves of *Fraxinus, Carpinus, Tilia, Ulmus* and *Betula* were commonly used for this purpose (Ellenberg 1978) and there is no reason to believe that this was not the case in earlier days. Thus the erradication of lime at the onset of the Sub-Atlantic could have been a purely artificial phenomena, probably of adverse consequence to the established human community that may have relied on this winter fodder source to a great extent. Perhaps a first case of over-exploitation of a natural resource, due to the inexperience of these early agriculturalists who had yet to develop and adapt more appropriate managerial strategies.

In the Iron Age the climate became much wetter, hence renewed peat formation. Oak pollen remains at similar quantities, thereby indicating that mixed farming was carried out on similar sized forest clearances and that the availability of more sophisticated iron tools did not bring about an immeadiately noticeable expansion of the settlement area. Fagus appears to have replaced Tilia on the valley slopes and has now become the commonest tree in the region whereas lime has completely disappeared and hazel is becoming progressively scarcer.

A renewed drop in oak pollen, roughly coinciding with the arrival of the romans in the area is evident on the absolute pollen diagram. Several Roman villas have been discovered on the Berdof plateau (Dondelinger 1861) and the proximity of a major roman city such as Trier are likely to have

required tremendous timber and firewood demands. The romans are also known to have introduced several plant species among which Juglans and Castanea may be the commonest ones. The pollen of former was only detected much later in the profile although seeds have been recovered in an archaeological context from a rockshelter site at Berdorf (unpublished data).

While oak appears to have been selectively removed as a high quality wood and to a lesser extent for increasing the agricultural land surface of the plateau, beech pollen is still found in large quantities. This may indicate that the slope forest remained on the whole undisturbed with regard to its integrity. However, in the subsequent spectra beech experiences a similar drastic decline which added to the higher frequency of dry land pollen may be indicative of a further opening of the plateau and valley landscape in relation perhaps, to a general increase in human population. Graminae, cultivation weeds and other dry land species are found more commonly and cereal pollen is found for the first time.

From the Dark Ages onwards it appears that most of the present day pattern of landuse and forest distribution already existed by then. Oak woods presently covering parts of the plateau may have been maintained artificially since the location close to the settlements and later the village as well as their role as a grazing and masting area for domestic animals would have been good reasons for preventing an eventual natural regeneration of beech.

The most recent development noticeable in the uppermost samples of the pollen diagram is the increasing importance of Picea and to a lesser extent that of Pinus in the vegetational composition of the region. These species have been planted increasingly since the nineteenth century and are most commonly encountered as monocultures. Furthermore, overall pollen concentration of most arboreal taxa was found to be markedly lower in recent spectra and this could be related to an intensification of the exploitation of wood resources notably for timber, charcoal and cellulose production during the eighteenth and nineteenth centuries and which may have involved the clearance of quite extensive areas of the valley forest.

From an ecological and botanical point of view, the most interesting finding observable during the Upper Postgalcial forest development may be the major fluctuations in Fagus and their possible relation to short term variations climatic (Slotboom 1963) or cyclical disturbance factors and long term population and ecosystem maturation. However, the pollen profile discussed here is not well suited for such detailed investigation and the discussoin has been deliberately limited to changes in the composition of plant communities. A second interesting observation, dealing precisely with such a major development concerns the coincidence in the area of the lime and hazel decline with the beech invasion, climatic deterioration and human activity. The latter has been dealt with above and attention will now be focused upon possible natural causes.

The rapid decline of *Tilia* and *Corylus* from the Sub-Boreal onwards is paralleled by the expansion of Fagus, a species with broad ecological amplitude. Capable of tolerating high amounts of shade, it can grow under an existing tree canopy and develop its own dense canopy, up to heights of over

30 m, over that of smaller trees, leaving little light to penetrate on the forest ground. Outshading may thus have been one means by which the newly arrived tree was able to eliminate the more light demanding lime and hazel plants.

Earlier on, it was mentioned that a tendency towards climatic deterioration followed by an accentuated increase in dampness and cold marked the period following the climatic optimum during which lime and hazel scored high values. And perhaps, this change in climatic regime could have adversely affected the existing lime population while favouring at the same time the establishement of any other tree capable of filling the niche hyperspace.

The failure of trees to regenerate can be related to several causes notably climate. Studies by Pigott and Huntley (1981) have shown that sterility of *Tilia cordata* throughout Britain and North Western Europe was caused by the failure of producing a fertile seed. Temperature was found to control whether or not fertilization occurs in natural conditions. The minimum summer temperature for *T. cordata* pollen to germinate is 15°C and maximal pollen germination occurs between 21°C and 18°C. If the temperature is too low then pollen tubes will only extend short distances into the tissue of stigmatic lobes and are usually arrested in the styles or in the ovary wall. There seems to be a clear need for adequate period of high temperature after flowering to allow insects to pollinate the flowers and pollen to fertilize the ovules. Sterility appears to be largely a consequence of events before fertilization although additional factors may further augment the risk. Damage to flowers by strong winds as well as a possible relation between ovular sterility and age of the trees may be additional limiting factors, although these are expected to apply only to particular years or local stands and may not explain the prolonged failure of regeneration observable on the pollen diagrams.

A further explanation may be suggested on the basis of edaphic factors. Presently most of the valley slopes are covered with a relatively deep sandy or loamy soils. These have developed form sediments transported and deposited along hillsides and covering underlying calcareous clays. The sites where *Tilia platyphyllos* has become to be regarded as native are on cliffs or steep rocky slopes. Small populations of the species grow on limestones, including the Carboniferous limestones in Wales and Derbyshire, the Permian magnesian limestone or dolomite of Derbyshire and Yorkshire, the screes of limestone in the Dordogne and steep slopes of limestone in the Swiss Jura.

The basic and generally calcareous nature of the soils in all these cases is consitent with the ecological behaviour of *T. platyphyllos* which is much more restricted than that observed for *T. cordata.* Large leaved lime is a tree of well drained basic soils especially of those which are calcareous in hilly regions of moderate rainfall. In these respects it resembles *Fagus sylvatica* although this species tolerates a much wider range of soils.

Studies by Pigott (1980) carried out in the Forêt de l'Eter close to Neuchatel in Switzerland have shown that there is ample evidence of lime regeneration in these situations as populations contain trees of all sizes and

are able to compete successfully with young beech trees. In contrast, though seedlings of broad leaved lime may be present on the deeper soils dominated by beech, saplings and mature trees are absent. The distribution of patches of lime trees within the National Park of Plivice in Yougoslavia has been investigated by Ellenberg (1978) and Pigott (1980), and both authors agree that the small populations of broad leaved lime occur in situations where the vigour and dominance of beech is conspicuously reduced.

If these ecological aspects derived from observations of modern day populations are accepted, then it may be suggested that edaphic factors involving the deposition of eroded colluvial and eluvial waste material down the valley hillslope may have confered a competitive advantage to beech, thereby causing the progressive exclusion of lime from the forest.

This scenario assumes that the lime woodland mainly consisted of *T. platyphyllos*. Unfortunately it was impossible to identify the pollen to species level. A distinction is possible but requires expert knowledge and detailed studies. However, isolated individual trees and small family groupings of broad leaved lime presently still grow in remote sites near the sandstone cliff and such stands may be regarded as relicts of the original lime population. The sandstone outcrops around the Berdorf plateau are very interesting from an ecological point of view in that this very diverse habitat has been a refuge for a relictual flora including the fern *Hymenophyllum tunbrigense* (Schwenninger 1988), *Pinus sylvestris* (Schwenninger 1987) probably lime and maybe juniper, heather and other plant species.

CONCLUSION

Holocene pollen records provide a fascinating perspective on long term forest dynamics and community structure that can not be obtained by looking only at modern plant assemblages, environmental conditions and ecological processes operating on time scales beyond human lifespans and research grants.

The measurement of pollen abundance as the pollen concentration of a unit volume of sediment avoids the constraints imposed by statistical interdependency of percentage calculations. This enables to detect changing abundances of plant taxa independently of each other and to observe interspecific interactions which cannot be done reliably with percentage data.

This study has demonstrated that some tree populations are considerably reduced when new taxa arrive while other populations are unaffected or may undergo selective pressure. Thus the appearance of pine after birch between 8000 b.c. and 6000 b.c. coincided with a reduction in the abundance of birch whereas the arrival of thermophilous deciduous taxa notably oak and lime between 6000 b.c. and 4000 b.c in turn caused a reduction in pine and later the immigration of beech has led to the exclusion of lime.

Other species such as hazel or oak have managed to maintain their populations in different types of communities (pine/hazel-hazel/lime-lime/oak-oak/beech) while a further group of trees managed to survive as small demes in refuge habitats after having become largely suppressed from their former range (pine, birch, lime and juniper on sandstone outcrops) or restricted to particular habitats (hazel along forest edges).

Some of these changes may be explained in terms of competitive replacements by more shade tolerant immigrants which forced more light demanding early pioneer trees, shrubs and herbs to become restricted to localized open areas such as the persistent belt of sandstone outcrop sand woodland margins or temporary open ground habitat. The flora of former may be viewed as relictual while that of local open grounds often comprises a weed flora following anthropogenic forest clearance.

Light is a primary resource for which trees compete and the replacements observed in the pollen spectra agree with what one would expect from a knowledge of their shade tolerances and the concept of competitive exclusion. However, shade tolerance is only one factor that may account for species replacements and other physical environmental factors such as climatic or edaphic changes during the Holocene are likely to have affected the competitive balances of tree species and their relative fitness. Furthermore, niche flexibility may allow some species such as hazel to adopt that of an 'understorey' ecotype, with reduced flowering and which may have survived until the present day, while the genotype determining the 'tree' phenotype may have become extinct (Bennett & Lamb 1988).

Pollen analytical work often is reduced to a descriptive account of the history of vegetational development that merely finds a use as a relative dating method. The value however of the pollen record is "that it identifies those interactions which are responsible for the composition of modern forests from the myriad of possible interactions facing an experimental ecologist who does not have the fossil record available" and "may miss vital clues to the basis of species richness and diversity in modern forests" (Bennett & Lamb 1988). Pollen data can document evidence for competition among species and suggest experiments to clarify the mechanisms of such interactions.

Forest composition has been shown to be unstable over long periods even though climatic conditions may only vary little and Clements (1916) principle of a climax community as a self-reproducing equilibrium in which species composition and other properties of the ecosystem would be relatively constant through time has been challenged. It is now clear that natural disturbances (fires, storm gaps, snow gaps, epidemic pest outbreaks, population moribundity, climatic fluctuations etc...) occur far more frequently and are much more important in forest dynamics than was allowed in the classic self-reproducing equilibrium type climax theory.

Forest composition is unstable and successional change viewed as stages through wave-like invasions by groups of species as a result of autogenic change is a 'facilitation' hypothesis. Successional change usually held to be orderely and therefore predictable has been defeated by reductionist theory

as a consequence of the defects and lack of applicability of the holistic approach. Succession thus is the sequential physiognomic dominance of a site by species with different life histories, growth rates, sizes, tolerance ranges and reproductive strategies (Finegan 1984).

On a more practical basis and from a conservation point of view it would be desirable to develop a protection and management scheme of wetland sites aiming at preserving not only animal and plant species but also the undisdturbed sedimentary sequence of their 'mud' deposits. These may be disrupted by heavy machinery used in forestry or by the earthworks of conservationists, seeking to maintain artificially a particular hydroseral stage suitable to aquatic plants and amphibians. Much the same may be said of archaeological sites that are a diverse and invaluable source of information about past environments but which are all too often destroyed as a result of large construction works.

Furthermore, it follows from the results of this study that local pine and lime stands are likely to be native and are hence worthly of conservation, especially as their natural habitat is adversely and increasingly affected by recreational activities and tourism.

The forest as we see it today, just as our modern society, is the result of past events which are responsible for what it is now. A woodland may be composed of individual components which are much older than the community itself and are therefore likely to long outlive it. A change either caused by a single or a constellation of interacting biotic and abiotic factors may be responsible for why a particular development has taken place from a panoply of possible pathways.

If we can discover and quantify the individual and synergetic influences and their impact upon the system we wish to study, whether this may be plant or animal communities, atmospheric circulation or human societies, then it should be possible to build a model which can be used in order to anticipate future events by simulating the systems behaviour and to explore alternative pathways by changing parameters.

There is no apparent reason to believe that the worlds climate is more difficult to model than plant and animal communities or human cultures although a knowledge of the evolution of the climate may have become of greater concern these days. Ultimately however one has to admit that climate is greatly influenced by living organisms and therefore a better understanding of these systems will improve our forecasts and insight into the functioning of "Gaia" (Lovelock 1988).

In order to survive and live the lives we wish to live, we can no longer cause major alterations to the environment without knowing about the consequences we risk to incur. In the words of John Lander Harper (1977) "One of the consequences of the development of the theory of vegetational climax has been to guide the observer's mind forwards. Vegetation is interpreted as a stage on the way to something. It might be more healthy and scientifically more sound to look more often backwards and search for the explanations of the present in the past, to explain systems in relation to their history rather than their 'goal'. "This statement implies that "the study of the

demography of long lived tree populations should involve a search for the past influences which have contributed to their present structure" (Ogden 1985). Retrospective techniques such as palynology combined with an experimental and modelling approach will be of great help in understanding vegetational and climatic processes and for managing the natural resources of our living planet.

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