THE SORTING OF PLANT REMAINS IN A RECENT DEPOSITIONAL ENVIRONMENT

by

Robert Andrew Spicer, B.Sc., A.R.C.S.

September 1975

A thesis submitted for the degree of Doctor of Philosophy of the University of London and for the Diploma of Imperial College

Geology Department,
Imperial College,
London SW7 2BP.

ABSTRACT

A Recent fluvio-lacustrine delta has been studied to investigate the relationship between deposited plant macro-remains and the living source vegetation. By using multivariate statistical techniques, lateral distribution patterns of plant remains entombed within the top 2 cm of delta sediment have been determined. These distributions may be related both to the dynamic processes of deposition and the relative positions of the source vegetation communities. A practical example, as well as the theoretical implications, of applying such quantitative methods to sampling in consolidated sediments is discussed.

The three dimensional nature of the deposit was determined by means of a series of cores taken with a 7.5 cm diameter piston corer and a general model for leaf deposition in such an environment is proposed relating the species composition of the resulting leaf assemblages to the source vegetation.

Experiments are described in which the biological and mechanical degradation of leaves of five tree species, Alnus glutinosa, Fagus sylvatica, Quercus robur, Betula pubescens and Salix cinerea have been studied during the first 8 months of deposition in both stream and lake environments, and the susceptibility to destruction by mechanical fragmentation has been experimentally tested. The use of X-ray microanalysis in the Scanning Electron Microscope to monitor element exchanges between the leaves and the surrounding sediment/water interface has been investigated. This early element exchange may well determine subsequent mineralization and has been studied using freeze fractured, freeze dried, transverse sections of individual leaves. The deposition of sediment films on the external surfaces

of leaves has been observed, a phenomenon which may well be the basis for many impression fossils.

By studying the early diagenesis of organic matter in this way, it has been possible to postulate the effect that similar species dependent breakdown is likely to have had in distorting fossil plant assemblages from the relationship with their original source vegetation.

CONTENTS

LIST OF FIGURES

APPENDIX

TABLES

APPENDIX TABLES

PLATES

ACKNOWLEDGEMENTS

The interdisciplinary nature of this work has necessitated consulting with a large number of people in a wide variety of subjects. To personally acknowledge all those who have given me advice or assistance would be impossible, but to them all I extend my sincere thanks. I would, however, like to especially thank Dr D.K. Ferguson for his stimulating discussion and whose enthusiasm is partly responsible for my interest in this aspect of palaeobotany. I am also grateful to Professor T.R.E. Southwood for allowing me to work on Silwood Lake, and to Professor F.H. Ludlam and his wife for the loan of their dinghy.

It is probably true to say that had it not been for the help of Mr P.R. Grant in all kinds of ways much of this thesis could not be written. To him and other members of the 'palynology' section I am deeply grateful. Special thanks are due to Mr R. Giddens for his brave assistance in the field.

Throughout this thesis reference will be made to the work of Dr C.R. Hill. I would like to take this opportunity of thanking him for his useful discussion and enabling me to utilize, so freely, his hard won data.

Much of the work presented here would not have been possible had it not been for the skill of the members of the Geology Workshop, in particular Mr E. Denman and Mr F. Chatfield, in making various items of equipment. In this respect, I would also like to thank Mr J.B. Steyn and Mr P. Giles for designing and making up the electronics for the apparatus for recording leaf floating times.

I am extremely grateful to both my supervisors, Dr M.D. Muir and

Dr K.L. Alvin, for all the useful discussion, help and encouragement they have given me, and for meeting the oddest requests for materials and equipment with good humour.

Finally, I thank the Natural Environment Research Council for financial support, Mrs Wendy Grant for her typing, and my wife, Ruth, for her support and encouragement.

INTRODUCTION

The development of any science follows a process of gradual change from a qualitative to a quantitative approach, and in this respect palaeobotany is no exception. Early collectors were mainly concerned with obtaining only the most perfect specimens and interest was largely esthetic rather than scientific. To this end professional collectors were employed solely to prospect for such fossils. As time went by the extensive range of morphologies exhibited by fossil plants became evident and gradually a more botanical interest evolved resulting in the development of techniques which enabled specimens to be examined in finer detail.

Eventually the paleobotanist began to do his own field collecting although a considerable subjective element remained, since only the best preserved, the atypical or the most conspicuous (usually the largest) specimens were collected. The museum specimen concept still survives, and probably always will do, but in the process of finding such a fossil a lot of valuable information is often either ignored or destroyed.

Any palaeoecological deductions based on specimens yielded by this approach must necessarily be subject to the distortions inherent in the haphazard sampling process, and may well lead to grossly inaccurate conclusions. Unless more systematic sampling methods are adopted such a state of affairs is likely to continue.

The palaeobotanist's traditional interest in anatomical and morphological detail for taxonomic and evolutionary schemes will always be of utmost importance since it is fundamental to the science. Recently, however, there has been a growing awareness of the necessity to investigate ways of extracting palaeoecologically useful data from

fossil deposits. A prerequisite of such an approach is the use of systematic (including truly random) sampling techniques and a change of emphasis from an analysis of the individual to an analysis of the population of fossils within an assemblage.

Early Work

The first example of systematic palaeobotanical sampling followed by a statistical analysis of the resulting data was carried out by Chaney (1924). He investigated the Bridge Creek flora of the upper Oligocene in Central Oregon U.S.A. and quantitatively compared the fossil assemblage with a modern redwood forest community which he considered resembled the orginal Oligocene flora.

The fossil deposit was sampled by excavating an area of rock some 15 feet long by 4 feet wide down to a depth of 1 foot and splitting the excavated slabs parallel to the bedding in order to expose the fossil leaves. These were then counted. Further excavations were made at two other sites, and, in all, 98 cubic feet of rock was excavated yielding a total of 20,611 specimens. In spite of this apparently large sample size, Chaney considered that perhaps no more than 75% recovery was being achieved. Chaney then asked the question "can it be assumed that the numbers of leaves and fruiting parts are an accurate indication of the relative abundance of the species they represent in the Bridge Creek forest?"

Such a question is clearly fundamental to any palaeoecological investigation and, as well as considering some general theoretical

factors*, Chaney attempted to supply the needed information by investigating what he considered to be a modern day equivalent of the fossil flora. Leaves on stream deposits within the redwood forest were sampled using 1 foot square quadrats. Leaf counts of the different species occurring within these quadrats were then compared with the number of trees of those species growing within a radius of 50 feet from each station. Correlation values between the deposited leaves and the numbers of source plants were then derived, and these were then used to estimate the number of source plants in the Bridge Creek forest that once grew within a radius of 50 feet from the depositional site.

Unfortunately, this promising piece of work was never seriously followed up until recently. Part of the reason for this was the lack of suitable statistical techniques with which to analyse the complexities of allochthonous assemblages, where extensive pre-depositional sorting has taken place. Chaney did not investigate any floristic pattern which might have been present within the volume of rock he excavated, and the entire excavation was regarded as a single sample. Part of the aim of

* Chaney identified these factors as being:

1) The distance of the species from the site of deposition.

2) The original thickness of the leaf, which he considered determined its ability to be transported without destruction.

3) The size and shape of the leaf as related to its transportation in both air and water.

4) The habits of the tree with regard to shedding its leaves.

5) The height of the stem of the plant, involving its aborescent, shrubby or herbaceous habit.

this thesis is to show that such pattern may exist and that it can be palaeoecologically useful.

Analysis of Quantitative Data

The developments of the quantitative approach in plant ecology has run parallel to a similar change of emphasis in branches of both earth and social sciences, and frequently similar statistical methods are employed. All are concerned with the analysis of situations where no single variable may be readily isolated, and the effect of this variable on the sample population studied. Often the causal factors of pattern within a data set cannot be readily identified. In such complex situations "there may be so many variables that the whole pattern cannot be intuitively grasped; if, however, the data can be so simplified that their internal interrelationships can be economically displayed, the investigator may, with greater confidence, suggest an hypothesis concerning the causal factors involved." (Lambert and Dale, 1964).

The aim of multivariate statistical analysis then is to simplify the data set in the most efficient way. A requirement for the successful use of any statistical technique is that it should be performed on a suitable data set, and that, if any valid conclusions concerning the sampled population are to be made, the data set should be appropriately collected. Special consideration to this problem is given later.

In plant ecology there has arisen a dichotomy of approach between classification and ordination, which has been the subject of extensive discussion in the literature (e.g. Greig-Smith, 1964, Lambert and Dale, 1964).

Classification involves arranging stands, or observations, into groups, the members of each of which have in common a number of characteristics setting them apart from the members of other groups.

Classification is to some extent an arbitrary process; such an approach is ideal for the taxonomist whose objective is to categorize a population in the most efficient and meaningful way. The desirability of the application of classificatory techniques to vegetation or fossil assemblages is, however, arguable. Greig-Smith (1964) points out that the taxonomist attaches great importance to the discontinuous characters or the organism he is examining. Similar discontinuous variables, for example presence or absence data, can be used to describe vegetation.

Lambert and Dale (1964) argue that the so called quantitative data of phytosociology is usually made up of qualitative and quantitative elements. This arises because, whereas presence or absence records form a self-contained logical system, the quantitative measures can only record the extent to which a species is present, not the extent to which it is absent. Quantification of a set of stands in which not all the species are present in all stands must therefore be a truncated quantification. This dissents from Greig-Smith's (1964) view that absence is an extreme of a continuous variable, which describes the amount of a species that is present. In Greig-Smith's opinion, classification of stands on the basis of species presence or absence tends to give either too broad or too narrow a classification for practical purposes, and one is forced to use quantitative, rather than qualitative, species estimates. Even though species abundance measures may be continuous variables, the characteristics of a population of stands may exhibit discontinuities. In spite of this, Greig-Smith (1964) has noted that even classification often suggests that vegetation varies continuously in composition.

The continuous nature of floristic pattern within a fossil plant assemblage is likely to be even more marked due to the complex interaction of physical, chemical and biological variables during transport, deposition and diagenesis. Reyment (1969) has noted that sedimentary

data contains a strong apparently random element, and recent work by C.R. Hill (1974) has shown that a large variation in species density between adjacent stands within an allochthanous plant bed is to be expected. Clearly the use of classificatory techniques under these circumstances, where data is forced into discontinuous groupings, may lead to highly erroneous results. For this reason clustering or classification methods are likely to be of little use in detecting floristic pattern in a fossil plant assemblage, and will not be considered further.

Alternatively, multivariate ordination techniques such as principal components analysis do not assume discontinuities within the data set. Rather, in an ordination of stands, an attempt is made to order the stands relative to one or more axes, in such a way that the relative position of a stand to the axes conveys the maximum amount of information about the composition of that stand (Greig-Smith, 1964). Thus a continuum is implied but this does not preclude the existence of discontinuities within the sample population and indeed, if these are present, they will be displayed.

The application of two ordination techniques, principal components ordination (P.C.A.) and Reciprocal Averaging (R.A.) (M.O. Hill, 1973), will be tested on both recently deposited plant remains and a fossil plant bed from the Yorkshire Jurassic. From this it is hoped that their suitability for detecting palaeoecologically important patterns in allochthonous populations will be determined.

Quantification in Palaeobotanical Studies

Although a quantitative approach has long been routine in the field of stratigraphic palynology, subsequent analysis of the resulting data has remained at the simplest level. Summary presentation has mainly

been in the form of histograms or pollen profiles, and considerable expertise in subjectively interpreting such diagrams has developed. While this approach was adequate for stratigraphic correlations, those workers interested in Quaternary palaeoecology recognized that meaningful palaeoecological conclusions could only be obtained providing adequate information was available regarding the different pollen productivities, dispersal, and deposition of the component species of the source vegetation. Perhaps the most important piece of work in this respect was that of Muller (1959) who investigated the pollen dispersal and deposition in and around the Orinoco Delta. This stimulating piece of work was followed by a variety of similar investigations of various depositional environments (e.g. Traverse and Ginsburg, 1966, and Peck, 1973).

It was soon realized that if reconstruction of past vegetational communities was ever to be achieved, generalized functional relationships had to be derived relating the number of grains of a particular taxon deposited in sediment to some measure of that taxon in the vegetation surrounding the site of deposition. One attempt to do this was by means of the correlation or 'R' value proposed by Davis (1963). By measuring the ratio of the pollen percentage of a species in a Recent depositional environment to the vegetational percentage of that species in the surrounding extant plant communities, fossil pollen percentages could be 'corrected' to give a measure of the species abundance in the ancient vegetation.

There are a number of serious flaws, however, in the use of the R value which have been discussed in the literature (Davis, 1969, Faegri, 1966). H.J.B. Birks (1973) stated that the most serious drawback is that the lateral extent of the vegetation contributing pollen to a medium or large-sized basin of deposition is generally not

known with any certainty, and thus it is impossible to delimit accurately the size of plot to be sampled in order to make comparisons between the fossil and Recent source vegetation valid. Only in deposits within closed forests or small basins can this problem be overcome (Andersen, 1970, 1973). Another variable is, of course, the structure of the source communites themselves and Janssen (1967) and Comanor (1968) have both demonstrated significant variations in R values for the same tree taxa occurring in different forest types (H.J.B. Birks, 1973).

Providing that reasonably accurate data concerning differential productivity of the various taxa is available (Andersen, 1970, 1973), a more fundamental approach to the problem of representation may be adopted by investigating the variables of dispersion. Tauber (1965) suggested a generalized model for pollen transfer in a forested area, and divided the pollen spectrum into a trunk space component, a canopy component and a rainout component. By considering the aerodynamic properties of the pollen grains in relation to the air flow near the ground and the position of the source relative to the depositional environment, the potential bias in the representation of the various deposited taxa could, in theory, be determined and suitable allowances made when considering the reconstruction of palaeocommunities.

Analysis of Recent pollen dispersal and deposition has become more sophisticated and now comprises an important branch of Quaternary studies. Multivariate statistical methods have also been used to analyse lateral distributions of pollen (e.g. O'Sullivan and Riley, 1974) and there is every reason to suppose such studies will continue. Oldfield (1970), however, introduces a cautionary note: "Elegance of technique or consistancy of results are secondary, for within a palaeoecological context, there is little point in studying pollen

production or dispersal at the present day purely as an end in itself."

Quantitative Macrofossil Studies

Recently quantitative assessments of macrofossil abundance have been used to supplement pollen data as it is generally considered that macrofossils represent only the local components of the flora.

The most notable of such studies was carried out by Watts and Winter (1966) who analysed the macrofossil content of cores, taken for pollen analysis, from Kirchner Marsh, Minnesota. The results were presented in the form of seed diagrams similar to those traditionally used for displaying the pollen spectrum. They found that broadly speaking many of the concepts of pollen analysis could be equally well applied to seed analysis, although they point out that seeds are not so suitable as pollen for statistical studies because they are less efficiently mixed in the seed rain. Such considerations are important both for stratigraphic correlations and palaeoecological studies, since conclusions based on a restricted sample from only a small number of cores could lead to erroneous conclusions. However, this heterogeneity in the macrofossil distribution (not only with seeds but also leaves and other remains) may well prove to be the forte of macrofossil analysis. The high degree of mixing that pollen and spores undergo during dispersal tends to destroy any pattern that might be used to determine the spatial relationships of the various sources. This, to a large extent, is not the case with the dispersal of macroremains.

As with pollen studies the application of multivariate statistical techniques to the analysis of macrofossil distributions has met with some success. H.H. Birks (1973) sampled some 32 lakes occurring in a number of different vegetational types. Surface samples of peat or mud were taken by hand or dredge. Known volumes of sediment, usually

50 cm^3, were then analysed for their macrofossil content and the numbers of each taxon expressed as numbers per 100 cm^3 of sediment. Macrofossil and vegetaional data was then analysed using Reciprocal Averaging (referred to in the paper by its French title 'Analyse factorielle des correspondences') and the resulting ordinations showed a close correspondence between the macrofossil content of the lake bottom muds and the surrounding vegetation. The pattern of macrofossil distributions within the lakes was also noted; there being a concentration of most species close to the shoreline.

The distribution of macroremains (including leaves) in a lake environment has also been investigated by McQueen (1969). Sampling was carried out at nine stations in and around a New Zealand lake. From simple tabulation of the data he concluded that in lake sediments the plant remains represent only the dominant members of the surrounding vegetation and no remains were found that had been transported any appreciable distance. However, in unimpeded rivers remains may be carried considerable distances and still remain recognizable. For instance it was concluded that a leaf of Nothofagus menziessii from a swamp site bordering the lake must have travelled at least 2 km down stream, but most of the distant taxa are filtered out by reed swamps and therefore never reach the lake bottom sediments.

Interest in transport, deposition and analysis of macrofossil assemblages has also come from palaeobotanists working on specific fossil plant assemblages. Ferguson (1971) studying the Kreuzau Miocene flora of Germany investigated the possible distances leaves could be transported by rivers before becoming so damaged that they were unrecognizable. By means of laboratory experiments rolling leaf discs, together with water and sand, it was concluded that damage by abrasion alone on fresh material was unlikely to cause serious destruc-

tion.

C.R. Hill (1974) investigated the practicability of quantitatively sampling fossil plant remains of the Yorkshire Jurassic flora exposed at Hasty Bank. Various points raised by this work will be considered in detail later.

Pfeiffer (pers. comm.) is at the present time investigating the lateral variation in plant distributions in shales above coal seams exposed in Indiana (U.S.A.) strip mines. As mining operations proceed 1 foot^3 samples are cut from the rock by means of a chain saw and analysis of the species content of the samples is carried out in the laboratory.

Krassilov's Classification of Palaeosuccessions

Krassilov (1969) proposed a scheme of classification of fossil deposits according to the processes that are supposed to have governed the floristic composition of the assemblage found within them. He observed that "every layer (of rock) containing plant remains is succeeded in the geologic section by a layer which a) does not contain plants, or b) contains mainly other plants, or c) contains mainly the same plants but in a different state of preservation, or with a different frequency of occurrence, or a different orientation in relation to the strike and dip." Krassilov then asserts that it is necessary to distinguish between changes due to real successions of the ancient vegetation and changes due to transport and burial.

His classification may be summarized thus:

Taphogenic palaeosuccessions - resulting from the selective characters of burial, transportability and strength of plant remains.

a) Selective Taphogenic - resulting from sorting during transport.

b) Lithification palaeosuccessions - resulting from changes in the composition of the buried vegetation assemblage in the course of diagenesis.

Cenogenic palaeosuccessions - due to the evolution and migration of floras.

a) Mutational Cenogenic - as yet to be recognized in the field but formed by the alteration of vegetation brought about by genetic changes.

b) Phenological - expression of seasonal variations.

c) Migrational - brought about by the migration of floras due to:

i) Topogenic factors - changes in topography and relief.

ii) Edaphogenic factors - changes in the soil characteristics.

iii) Climatogenic factors - climatic changes.

While such a classification has its uses, its rigid application invites over simplification of the processes involved in determining the species composition of an assemblage. More than one type of palaeosuccession may occur in the same deposit and a merging of one type with another, both vertically and horizontally, is probably more common in nature than is at first realized. Indeed the logical consequence of the leaf deposition model that will be presented later in this thesis is just such a situation where, at deposition, taphogenic and topographic/edaphic palaeosuccessions merge laterally, while subsequent diagenetic changes introduce the possibility of a lithification palaeosuccession being formed. Such a classification may be useful when describing large scale depositional regimes, but its application to individual deposits is doubtful.

This then forms the background to the present study. The quantita-

tive analysis of fossil plant assemblages to give palaeoecologically meaningful information is clearly in its infancy. Before going too far forward, however, particularly in the development and application of sophisticated numerical techniques, it is necessary to ask some basic questions such as: What is it we are trying to measure, what are the factors involved in distorting the information we collect from the information that was potentially available in the living community, and how is it we can obtain the most objective and efficient sampling of a fossil deposit?

Clearly, answers to these and similar questions involve a wide range of considerations from the measurement of extant vegetation (without using the type of information that is, by its nature, unavailable in the fossil assemblage), the mechanics of transport and deposition, through the fossilization process to the sampling of the fossil population and its subsequent mathematical analysis. The aims of this thesis, then, are to evaluate the effect on palaeoecological information of these processes using a modern depositional environment as a working system, to erect a generalized model of deposition of macroremains in such an environment, and to show how existing mathematical techniques can be used to reveal meaningful patterns of plant distributions in both modern and fossil deposits.

THE FIELD SITE

The modern depositional environment chosen for this study was a fresh water lacustrine delta in the grounds of the Imperial College Field Station at Silwood Park (Grid Ref. SU941691). Rocques' Survey of Berkshire (1761)* does not figure a lake in the area of what is now Silwood Park, only a stream. An enclosure map of 1815, printed by Benjamin Badcock of Oxford,* shows a lake, however, much larger in extent than at present, extending as far as Cascade bridge towards the south west (Fig. 1), while on a geological map of 1819 by William Smith no lake is shown. It is likely that an existing, possibly slightly out-of-date, map was used as the basis of the geological map and thus the date of the construction of the lake may be reasonably supposed to have been just prior to 1815.

The lake was artificially constructed by damming the north eastern end of the existing valley. Originally it was thought that the lake had been 'puddled' to prevent drainage though the underlying porous Bagshot sands, but cores taken in the delta area show a continuous clay lining to be absent. A spring line at the bases of the surrounding hills indicates that the water table in the Bagshot sands is locally higher than the water level in the lake, thus obviating the need for an impervious clay lining.

From the extent of the open water, as delimited in the 1815 enclosure map, it appears that the majority of the S.W. arm of the lake has, since that time, filled with sediment brought down by the stream (Fig. 1). The present delta front is some 60 m or so wide and approximately 300 m N.E. from Cascade bridge. If an estimate of an average sediment depth of 2 m is used, then a total of approximately

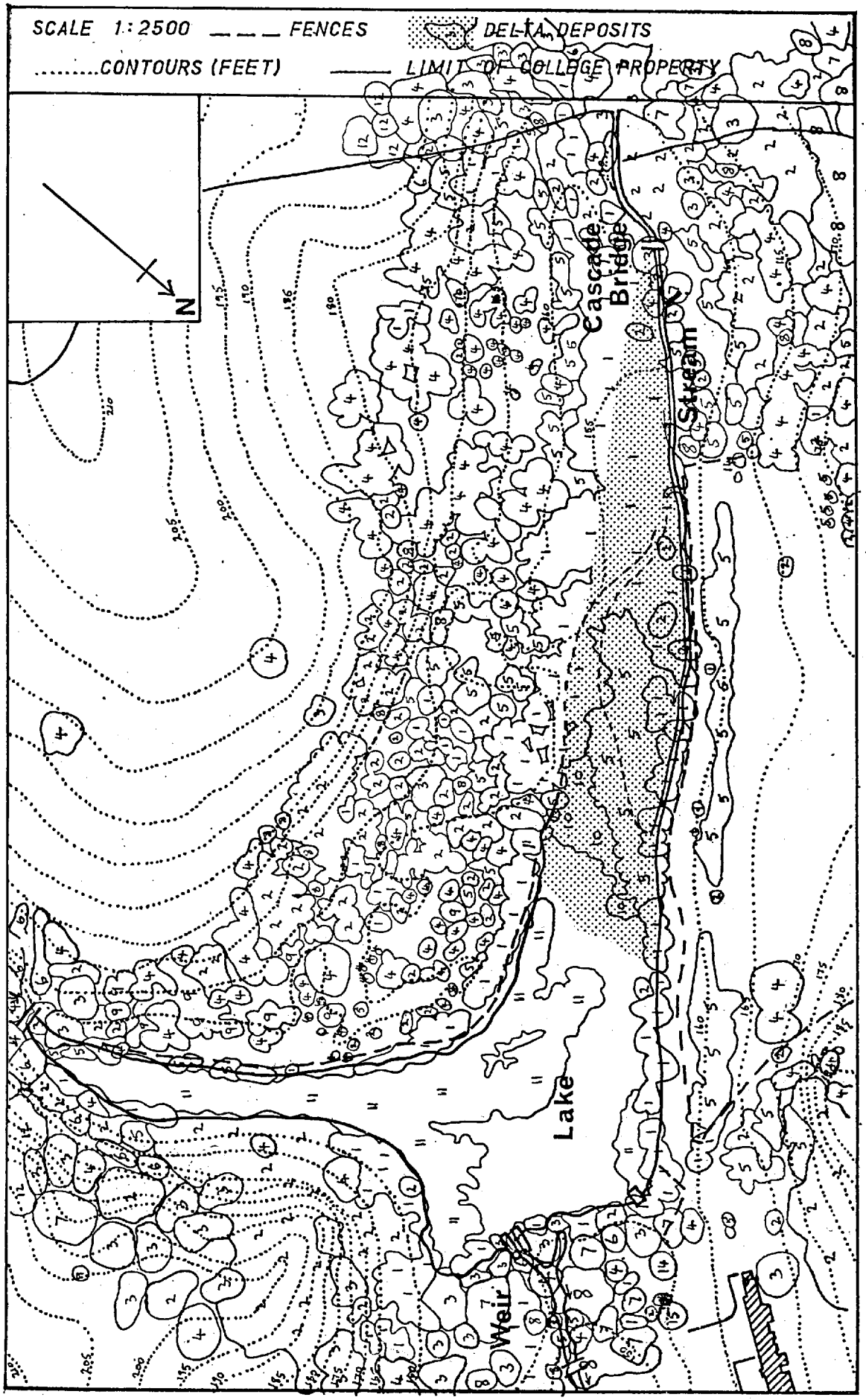
* Berkshire County Records office.

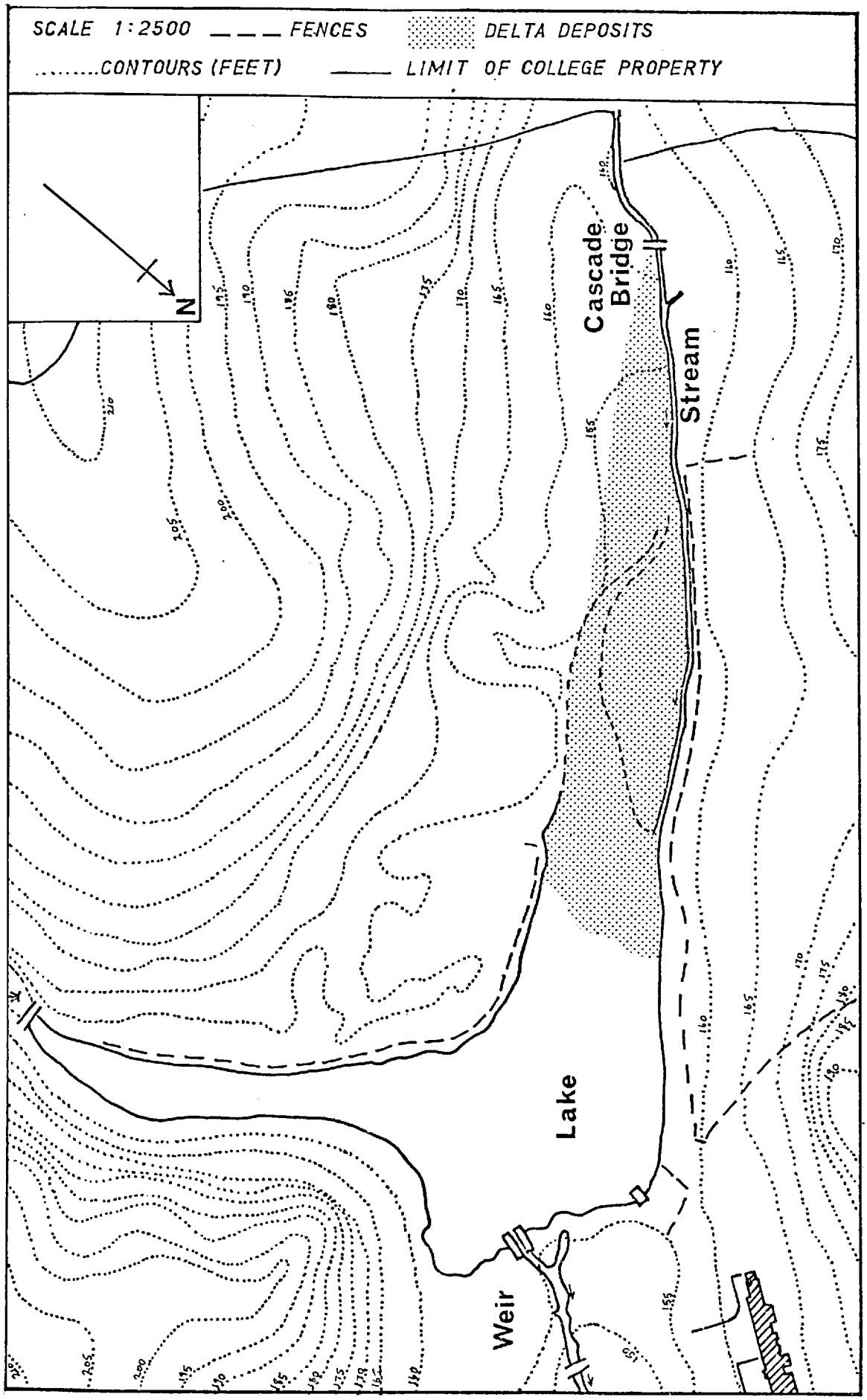
Fig. 1 (opposite) A topographic map of the area immediately surrounding Silwood Lake. The stippled area indicates the extent of the deltaic deposits.

Fig. 2 (overlay) The positions of the tree species comprising the canopy, as seen from the air, are shown as well as the extent of Typha and Nuphar. The taxa are numbered as follows:

1) Alnus glutinosa (L.) Gaertn.
2) Betula pubescens Ehrh.
3) Fagus sylvatica L.
4) Quercus robur L.
5) Salix cinerea L.
6) Ilex aquifolium L.
7) Aesculus hippocastanum L.
8) Acer pseudoplatanus L.
9) Crataegus monogyna Jacq.
10) Typha latifolia L.
11) Nuphar lutea (L.) Sm.
12) Castanea sativa Mill.
13) Salix alba L.
14) Fraxinus excelsior L.
15) Pinus sylvestris L.

Except where the canopy is continuous the approximate size of the crowns are indicated.


SCALE 1:2500
FENCES
DELTA DEPOSITS
CONTOURS (FEET)
LIMIT OF COLLEGE PROPERTY
N
Cascade Bridge
Stream
Lake
Weir


SCALE 1:2500
FENCES
DELTA DEPOSITS
CONTOURS (FEET)
LIMIT OF COLLEGE PROPERTY
N
Cascade Bridge
Stream
Lake
Weir

18000m^3 of sediment has been deposited since about 1800 A.D.; a rate of around 100 m^3 per annum. The majority of this delta deposit now supports a well developed Alnus glutinosa (L.) Gaertn. Carr. (Plate 1).

The existing weir was constructed in 1958 and now maintains the lake level constant to within a few centimetres, although during construction of the weir the lake was partially drained for sometime.

It is known that the stream supplying sediment to the S.W. arm of the lake has been artificially straightened (Mr E. Green, pers. comm.) although no accurate date for this event is available. It would appear that previously the stream emptied into the lake more to the South of its present inflow and during the period of this study (October 1972 - October 1975) it was seen to revert to this position after periods of heavy rain. The stream frequently crevasses the partially natural levees along the last 300 m of its length resulting in the periodic flooding of large areas of the compacting delta sediment.

Though small, of course, by comparison with many bodies of fresh water (surface area approximately 13000 m^2) Silwood lake is of the same order of size as many fossil leaf deposits. (e.g. the Tennessee clay pits described by Dilcher, 1971, and the Kreuzau deposits described by Ferguson, 1971). Both of these floras are supposed to have been laid down in an ox-bow type of lake. Such an environment may well be conducive to the fine preservation exhibited by fossils from both localities, but unfortunately it is unlikely that this type of deposit will yield significant information concerning distant floras since these basins are isolated from flowing water, except during flood periods, and are restricted to the flat topography of flood plains where vegetational diversity is likely to be small.

Although the natural processes of lake basin formation are many and varied, lateral lakes of a large river system provide situations

similar to that of the Silwood environment. These lakes are formed when sediments of a large river are deposited as levees and back-up water in a tributary stream. Examples of such lakes are Lake Tung-ting and other lakes of the Yang-tse-kiang, lakes of the lower Danube and lakes of the Red River in the Mississippi drainage (Hutchinson, 1957). The deposits of such lakes are likely to yield fossil leaves derived from both riparian and slope vegetation. Thus, in spite of the artificial nature of the Silwood lake and the present stream course, natural processes of transport and sedimentation are considered to be in operation.

PLATE 1

Above - Part of the Alnus Carr that has developed on the consolidated delta.

Left - The stream flowing towards the lake as viewed from Cascade bridge.

MATERIALS AND METHODS

ANALYSIS OF THE VEGETATION SURROUNDING SILWOOD LAKE

It is clear from the literature (e.g. Newbould, 1967 and Hughes, 1971) that to obtain a representative estimate of the total litter production, by an area of vegetation as extensive as that surrounding Silwood Lake, would be a major task and take many years. It was not, of course, feasible to undertake such a project in the course of this present study, but it was possible to map the position of every tree species that comprised part of the canopy and, in this way, estimate the relative potential source areas for the different species of deposited leaves. An aerial photograph (Aerofilms HSLUK:71173) taken on 8 September 1971 was used as the basis for a vegetation map, and by ground survey the species of every tree seen from the air was determined and plotted as shown in the overlay (Fig. 2).

The vegetation map was then divided into regions of interest at various distances from the delta. This was done by scribing circles of 2, 4, 6, 8, 10, 12, 14 and 16 cm radius (equivalent to 50, 100, 150, 200, 250, 300, 350 and 400 m full scale) from the delta front centre and measuring (using a 1mm grid) the areas of the canopies of the various species lying between successive circles. The percentage area of each species, within each ring, was then calculated. The areas of each species in all the regions of interest were then progressively summed, and successive percentage areas for the species within the complete circles of increasing radii were calculated. The percentage species composition for the circle equivalent to one of 400 m radius full scale was then taken as being representative of a summary of the vegetation in the field area. The results are shown in table 1, (p.84).

Delta leaf traps

To determine the proportions of leaves of the various species deposited on the delta surface by direct wind transport, fifteen water leaf traps were positioned on the delta shown in Fig. 3. The trap frames were constructed of wood to the dimensions shown in Fig. 4. '1000' grade polythene sheet was then put over the frames and pinned to form a shallow watertight tray 5 cm deep and 0.5 metres square. A small hole was then made in one corner, close to the top of the wooden frame, to allow excess rainwater to overflow without washing out any leaves. The traps were then staked in position on the delta (Fig. 3) at coordinates obtained from a random number table (Fisher and Yates, 1963), and filled with water. At frequent intervals between mid-September 1973 and mid-November 1973 leaves were removed from the traps by means of a small net, placed in plastic bags, and stored in 5% aqueous formaldehyde until such time as they could be counted. The water level in the traps was topped up when, and as, required.

Leaf traps of similar design were originally staked at 15 m intervals along the inflow stream and the leaves collected on a weekly basis. It was hoped that in this way an estimate of the litter fall, as intercepted by the stream, could be achieved. It was soon found, however, that at periods of bankfull discharge many traps, laden with leaves, became swamped, and the trapped leaves either washed out, or the samples were contaminated with waterborne leaves.

The adoption of regular trap spacings along the stream, was, on reflection, ill considered; they should have been randomly positioned. In view of these problems the experiment to estimate litter input to the stream was abandoned. Some of the leaves that were collected, however, were retained for size comparison with the lake samples.

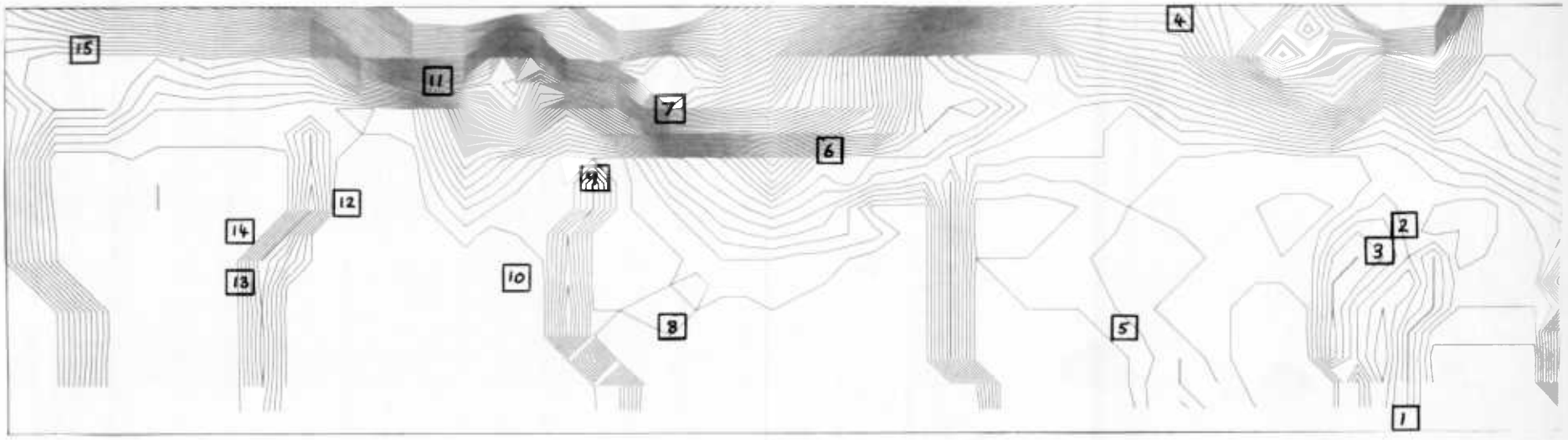
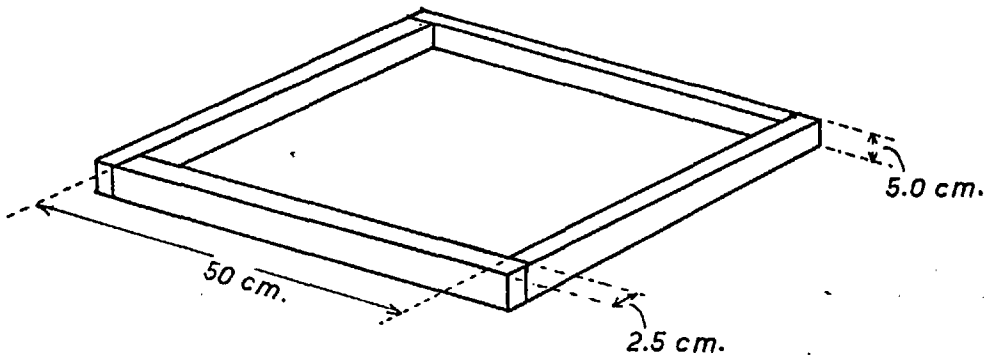
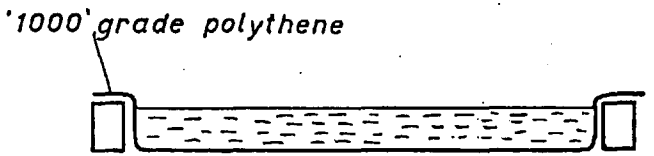


Fig. 3. The positions of the leaf traps on the delta. For an explanation of the contour map see Figs. 7 and 8 and the text.

Fig. 4. Construction of the leaf traps. Wooden frames were constructed to the dimensions shown and lined with polythene sheet as depicted. The shallow tray so formed was then filled with water. The bouyancy of the wooden frame ensured that even when the trap was positioned in open water the edges were clear of the water and thus leaf exchange in and out of the trap was prevented.





The numbers of leaves of the different species falling into the delta traps were determined and the results are displayed in table 2.

The areas of undamaged Fagus and Alnus leaves that had been caught in the delta traps were measured using a Paton electronic planimeter and compared with samples of leaves caught in the stream traps. The results are presented in Figs. 22 and 23. The stream and delta samples were compared using a Fisher-Behrens test as described in Campbell (1967).

Wind Data

Surface wind directions and strengths for July to December 1973, as measured at Heathrow Airport (8 miles to the N.E. of Silwood Lake), were obtained from the British Daily Weather Reports. It was assumed that these readings would also serve as an estimate of the wind conditions at Silwood Park, although local topography may have slightly modified the wind patterns around the lake. The wind direction and speed was recorded four times in every twenty four hours.

Each wind direction reading was weighted by the appropriate wind speed (measured in knots) and from this data the mean wind direction for every week was calculated (Fig. 21). Weighting by wind speed was employed since it may be argued, for instance, that a strong wind exerts more influence on wind dispersal than a gentle breeze. However, no corrections were made for periods of rain which could have reduced wind dispersal. The weighted wind direction data was processed using the program ORIPAL as published in Reyment (1971).

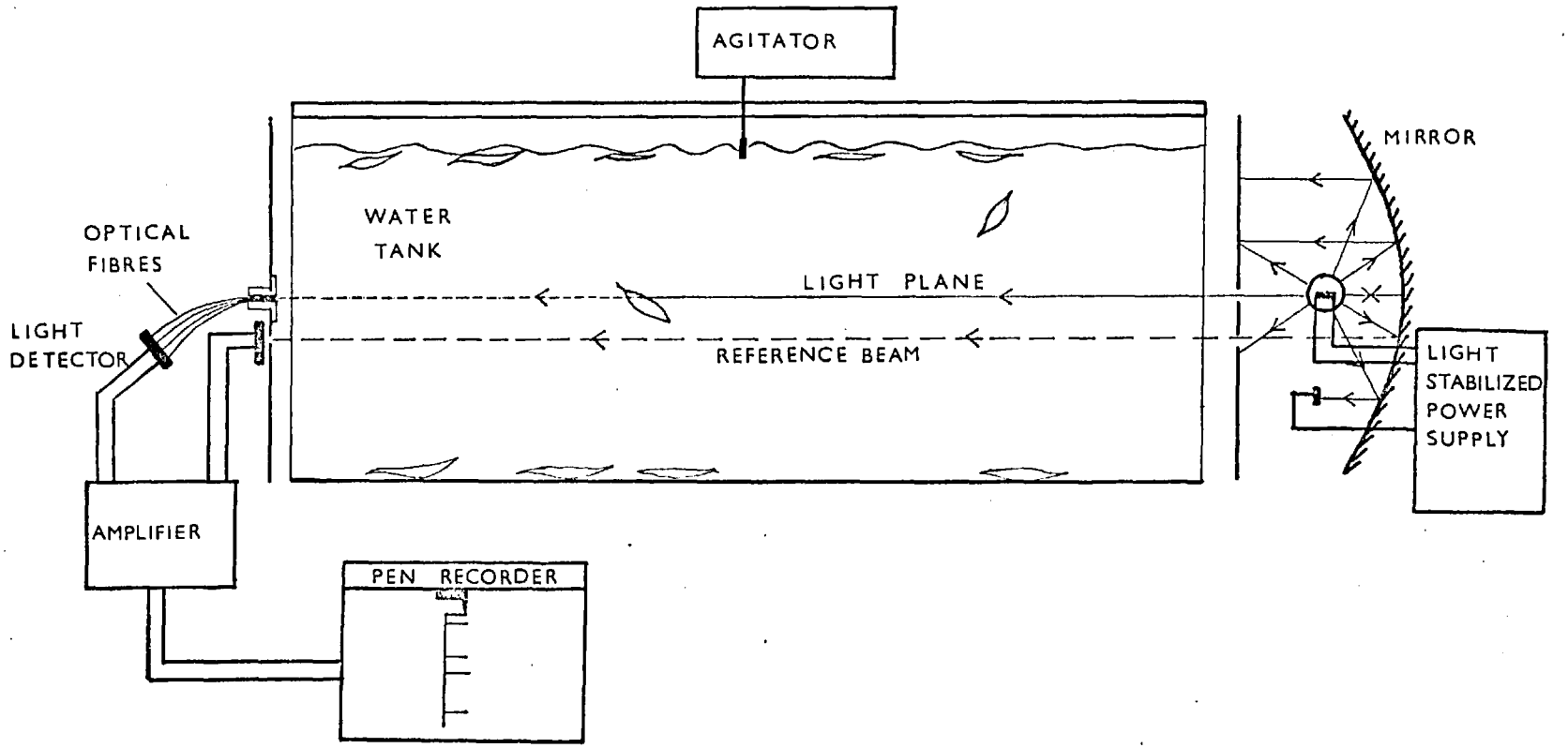
MEASUREMENT OF LEAF FLOATING TIMES

In order to estimate the relative leaf dispersal that could be attributed to differences in leaf floating times, the following experiments were carried out.

Samples of freshly fallen leaves from trees and shrubs growing around Silwood Lake were collected, returned to the laboratory and dried at room temperature. A known number of leaves of each species (usually 50) were then taken and put into buckets that were three quarters full of tap water. At various times during the course of the experiment the leaves were stirred round in the water and left to settle, after which, the number that remained floating were counted. It was soon realized that with those species where most leaves sank within two days large errors were incurred by not having any readings during the night. To try and overcome this problem the following apparatus (diagrammatically shown in Fig. 5) was constructed.

A 12 volt car headlamp bulb was positioned at the focus of a concave parabolic mirror and powered by an optically stabilized rectified power supply. By means of a collimation slit in front of the bulb a parallel plane of light was made to pass down the length of a rectangular glass aquarium, in such a way that any object sinking in the tank would interrupt part of the beam. A line of optical fibres was then positioned, normal to the glass, across the width of the tank, at the opposite end to the light. The free ends of the fibres were then formed into a bundle and abutted against the sensitive surface of a selenium light sensitive resistor. The light cell was then connected to an amplifier and thence to a pen recorder. In this way, the moment that any sinking leaf cut the plane was recorded.

Fig. 5. Diagram of the light plane apparatus for recording leaf sinking events. For explanation see text.



To compensate for any discolouration of the water, brought about by leaching of compounds from the leaves, a reference beam was set up to pass through the water down one side of the tank and the receiving light cell was balanced with the one receiving the light plane.

It was noted that unless leaves were intermittently agitated gas bubbles formed on them which prevented them sinking even though they were waterlogged. A mechanical agitator was then constructed to periodically generate riples on the surface of the water. In practice it was found that even slight agitation of the water caused previously sunken leaves, with a buoyancy only slightly in excess of neutral, to be stirred up and intercept the light plane. For this reason the use of the apparatus was unfortunately limited. A deeper tank would no doubt have overcome this problem but one was not available.

LEAF DEGRADATION EXPERIMENTS

The relative degradation rates of leaves of Quercus robur L., Fagus sylvatica L., Betula pubesceus Ehrh., Salix cinerea L. and Alnus glutinosa (L.) Gaertn. were investigated in the experiments described below. In the remainder of this thesis usually only the generic names for these plants will be used, except where confusion could arise.

Three hundred and sixty freshly fallen leaves of Quercus, Fagus, Salix, Betula and Alnus trees, all of which were common in the field area, were collected in the autumn of 1973 and returned to the laboratory. Here they were dried at room temperature for 21 days. 75 leaves of each of the taxa were then placed in each of four rectangular nylon cages (25 x 25 x 6.5 cm) constructed of 5 mm^2 mesh 'Netlon'. No metal was used in the construction; all seams being made with nylon thread. Two cages were then weighted (with iron ballast sealed in a '1000' gauge polythene bag so that the leaves could not be contaminated by the ballast), and deposited on the bottom of the lake, while the other two cages were tied to a wooden stake in the stream. The wooden stake was not treated with preservative or any other 'foreign' compound.

After periods of approximately 1, 2, 4, 6 and 8 months, samples of 25 leaves of each of the species were removed from the cages and returned to the laboratory where they were processed as rapidly as possible. The first three samples (months 1, 2 and 4) were taken from the same cages in each environment, and the remaining samples from the other. It had been originally planned to take a sixth sample at 12 months but by this time only Fagus and Quercus leaves

remained in the stream cage. Also the polystyrene foam buoy, which marked the position of the lake cages, could not be located, hence recovery of the lake samples was made impossible.

On return to the laboratory five leaves of each species were taken for X-ray microanalysis (see page 65). The remaining twenty leaves of each species were used for leaf degradation studies. The leaves were carefully washed to remove loose sediment and the extent of natural leaf degradation was recorded, either by photo-copying, or by tracing the outline. In this way the extent of lamina loss, primarily due to biological agencies, in the relatively protected environment of the nylon cages could be determined. The mesh of the cages was such that free access to the majority of aquatic invertebrates was afforded, while retaining all but the smallest leaf fragments. The degree of breakdown of the various species is shown in Figs. 28-43.

The washed leaves were then loaded into the drum of the rolling apparatus (described below), together with 2.5 litres of tap water, and rolled for 90 minutes. From preliminary experiments, using both fresh leaves and leaves collected from the stream bed, it was found that this treatment only minimally damaged fresh leaves, while leaves from the stream were highly fragmented. It was, therefore, considered that such treatment would yield a range of fragmentation representative of the leaf degradation state.

All species from the first two sampling dates were rolled together, but the last three could only be treated separately since a large number of fragments were generated and subsequent identification of the fragments became extremely tedious. The resulting fragments were then stored in 5% aqueous formaldehyde solution until such time

as they could be counted and, in some cases, their areas determined using a Paton electronic planimeter. Only the areas of fragments from the leaves receiving the shortest exposure to the lake or stream environments could be measured because a drop in accuracy was found when measuring large numbers of small areas.

Description of the rolling apparatus

The apparatus (Fig. 6) consisted of a plastic drum (class 'B' pressure pipe supplied by Osma Plastics) 22 cm in diameter and 36 cm long (A) with 1.2 cm thick removable 'Perspex' ends (B and C). The drum was fitted with cylindrical wooden paddles (D) as shown in the diagram. The drum was supported on two rubber clad rollers (E) (external diameter 17 mm) one of which was driven at constant speed by a $\frac{1}{4}$ horse power electric motor. The drum rotated at a rate of 70 revolutions per minute. A watertight seal between the drum and the end plates was achieved using 'Sealastic' sealing compound.

The purpose of including the wooden paddles was to provide turbulence and obstacles against which the leaves would knock, similar to branches and other static objects likely to be found in a small stream. It was not intended, however, that the experiment should simulate any particular stream, but rather to expose the leaves to some of the forces likely to be found in nature. The water energies the leaves would experience within the drum were, for instance, fairly high, but this ensured that fragmentation was as rapid as possible in order that the effect of continued, indeed accelerated, microbiological activity under the relatively warm laboratory conditions was minimised during the rolling period.

Figs. 44-46 show histograms of the frequency distributions of the various fragment areas produced by rolling. At first it was

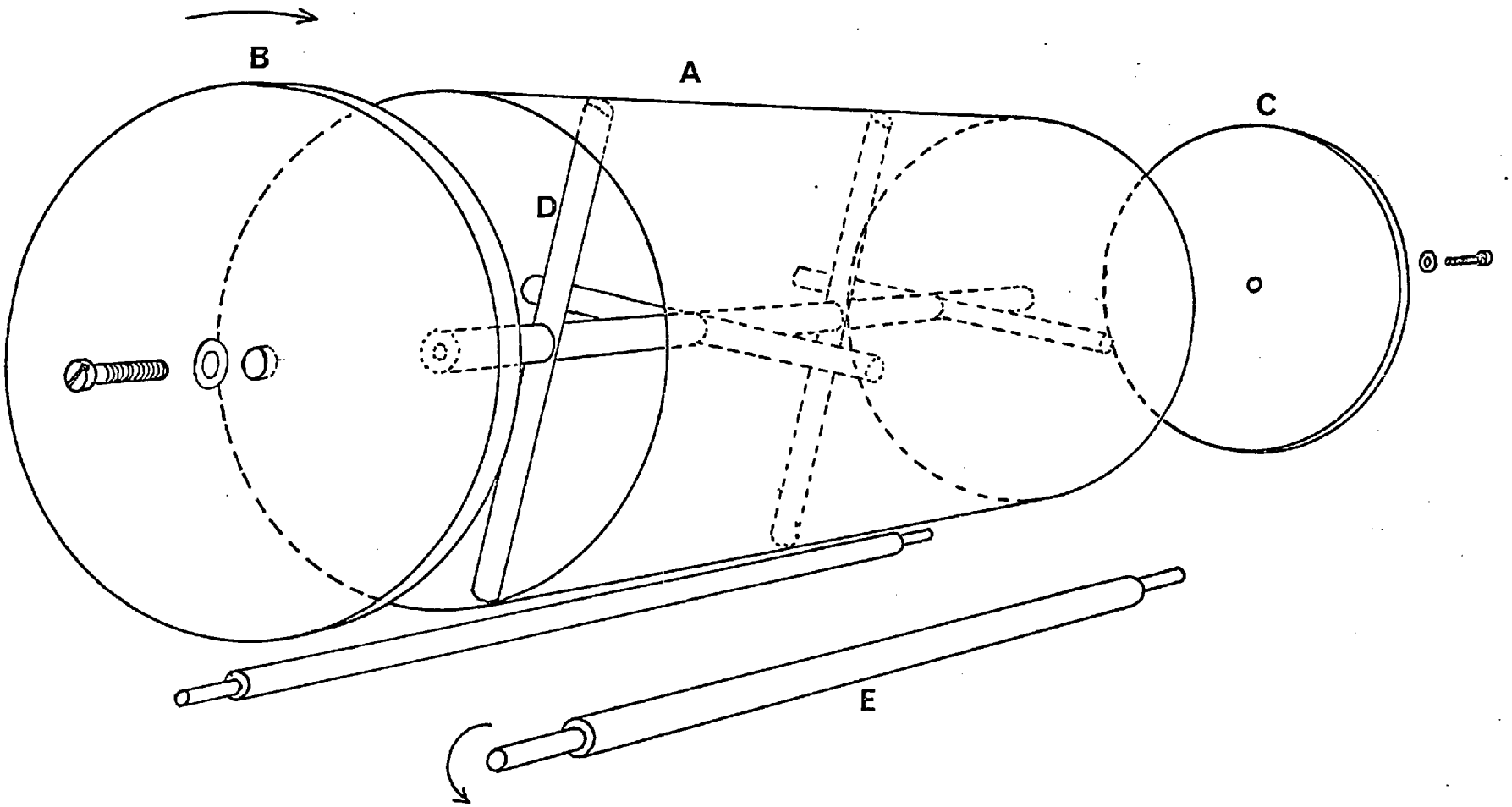


Fig. 6. Diagram of the leaf rolling apparatus. For explanation see text.

thought that an adequate representation of the relative fragmentation might be assessed in terms of the percentage shift in the mode or median of the distributions. However, examination of Figs. 44-46 reveals that the distributions are in fact bimodal. It appears that the peak at low size classes represents large numbers of small fragments that are produced by attrition. The remnants of the whole leaves form the peak at the larger size classes. In view of the bimodal distribution a more suitable way of expressing fragmentation was considered to be average fragment area, after rolling, divided by the original average whole leaf area. This fraction was then expressed as a percentage. The fragmentation of leaves so expressed is presented in Figs. 47-50.

LEAF DISTRIBUTIONS IN THE DELTA SURFACE SEDIMENT

The lateral distribution patterns of deposited leaves within the surface sediment of the Silwood delta were investigated in the following way.

A grid was laid out on the delta by means of parallel lines of string 2 m apart, each line being marked off into 2 m lengths. In this way accurate sample location was achieved. Access to the delta was afforded by a flat bottomed dinghy from which, as well as sampling, water depths were measured using a weighted measuring tape. The resulting bathymetric matrix was used to generate computer drawn contour maps (Fig. 7) and three dimensional profiles (Fig. 8) of the delta surface.

Samples of the leaves entombed in known volumes of sediment were taken at the positions indicated in Fig. 9. Species/area curves were initially constructed using rectangular wire quadrats and from this data a sample area of 0.5 m x 0.5 m was chosen as being most suitable. An arbitrary sediment depth limit of 2 cm was then chosen for each sample. Replication of the sampling volume was achieved by using the aparatus shown in Fig. 10. A sheet metal frame (A) was constructed 0.5 m x 0.5 m square with external lateral 'wings' (5 cm wide) which prevented it sinking into the sediment during sampling. 2 cm below these wings, on the inside of the frame, were two ledges along which the cutting edge of the sieve quadrat (B) ran. After positioning the frame in the sediment, the sieve quadrat was pushed into the frame, and then carefully lifted out, so that a sample of sediment 0.5 x 0.5 x 0.02 m was retained on the sieve quadrat. The sediment was then carefully washed through the sieve (0.5 cm^2 mesh), leaving the plant

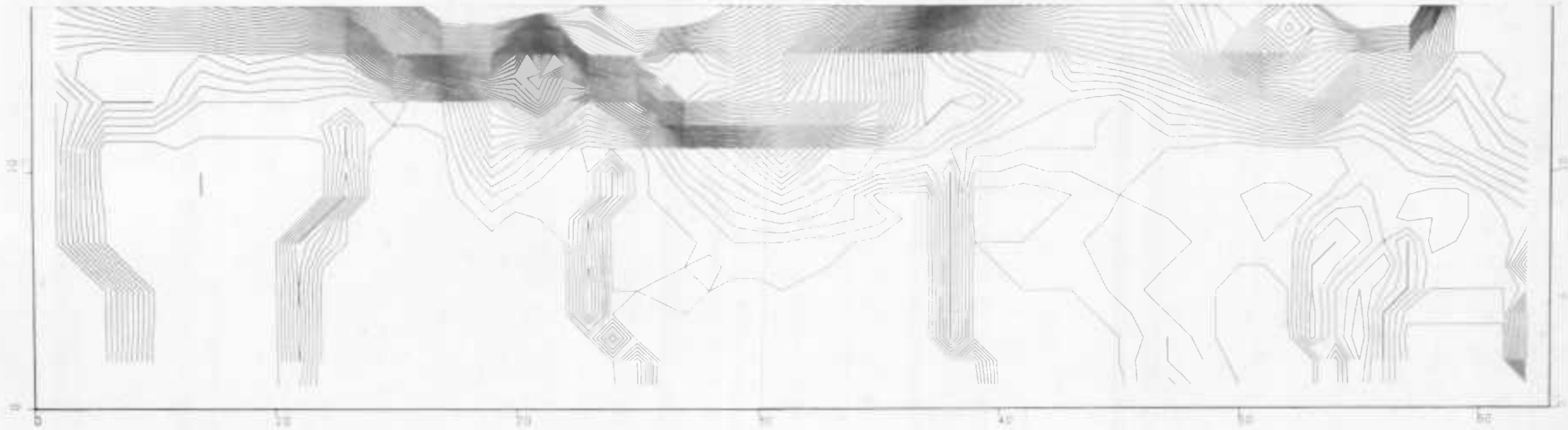


Fig. 7. A computer drawn contour map of part of the Silwood delta. The contours are drawn at 1 cm intervals and depict the subaerial part of the delta as well as most of the prodelta slope. The edge scales shown are in metres. The map was constructed from a regular bathymetric matrix using a Fortran IV program 'Contour' written in the Geophysics Department of Imperial College. Because of the difficulties of labelling each contour line a three dimensional representation of the delta, drawn from the same matrix, is presented in Fig. 8 as an aid to interpretation.

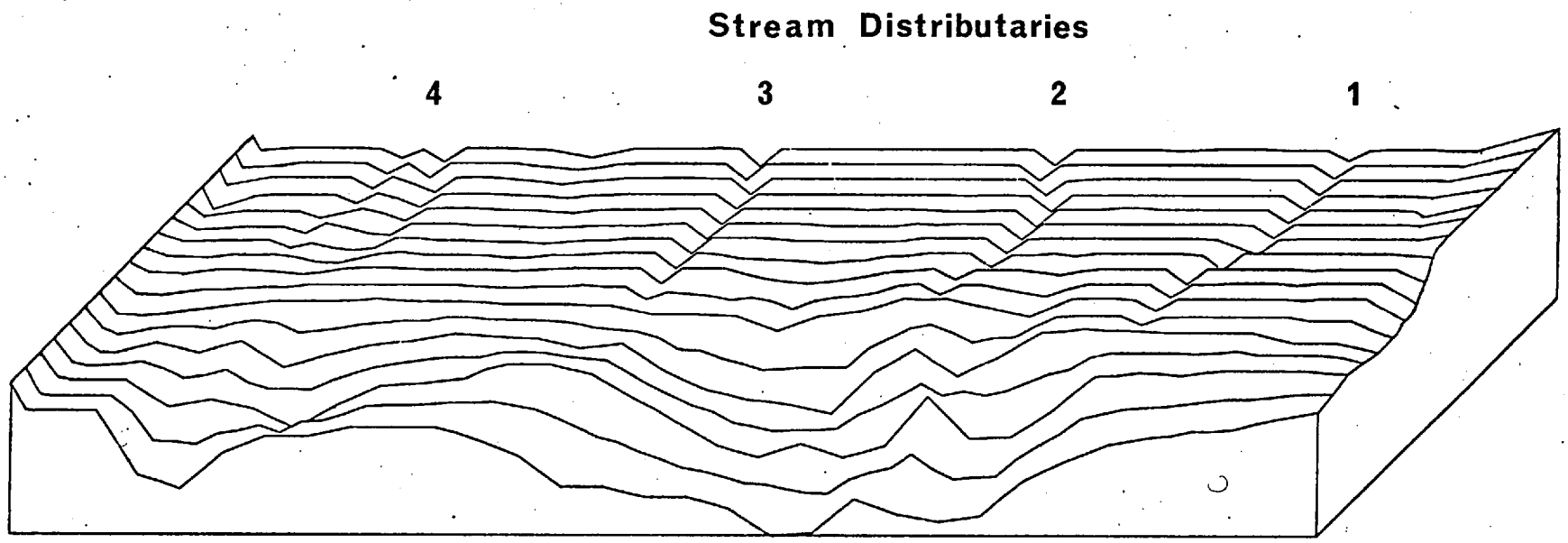
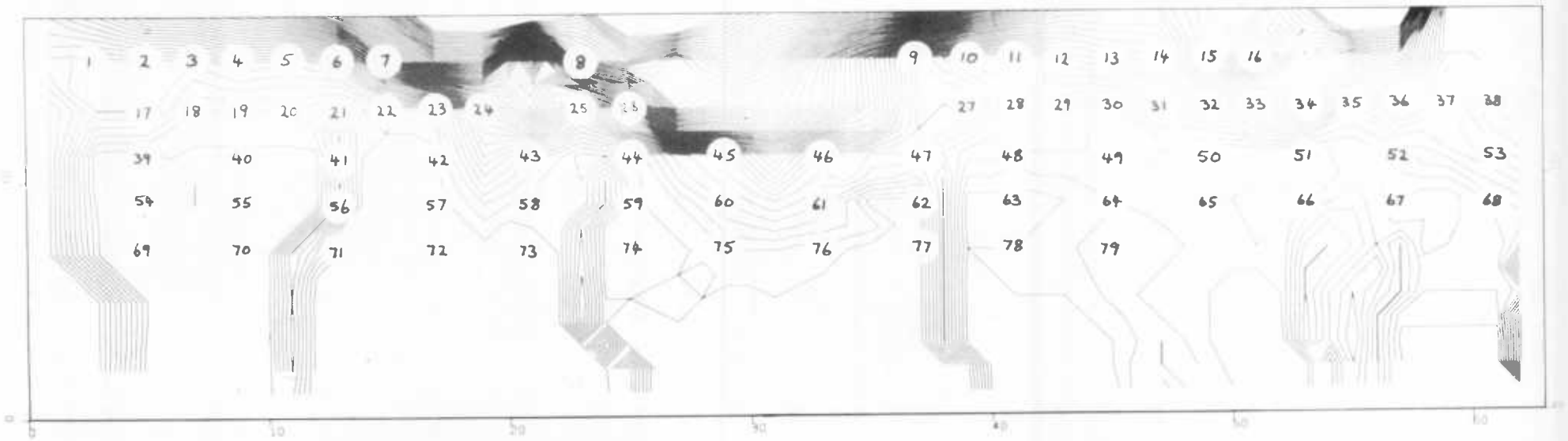


Fig. 8. The above 3D representation of the delta was drawn using the 'Block' mapping program of the matrix mapping package 'MATMAP' available at Imperial College Computer Centre. The delta is viewed from above the northern shore of the lake. The relative importance of the distributaries was visually assessed, and is expressed in terms of the percentage of the total stream flow that they carried during the period of sampling. Distributary 1: 50%, 2: 30%, 3: 20%. Distributary 4 was not directly connected to the inflow stream and only carried what was considered to be run-off and seepage from the south bank.

Fig. 9. The diagram below shows the positions of the leaf samples from the surface sediment of the delta which were collected using the sampling frame shown in Fig. 10 and Plate 2.



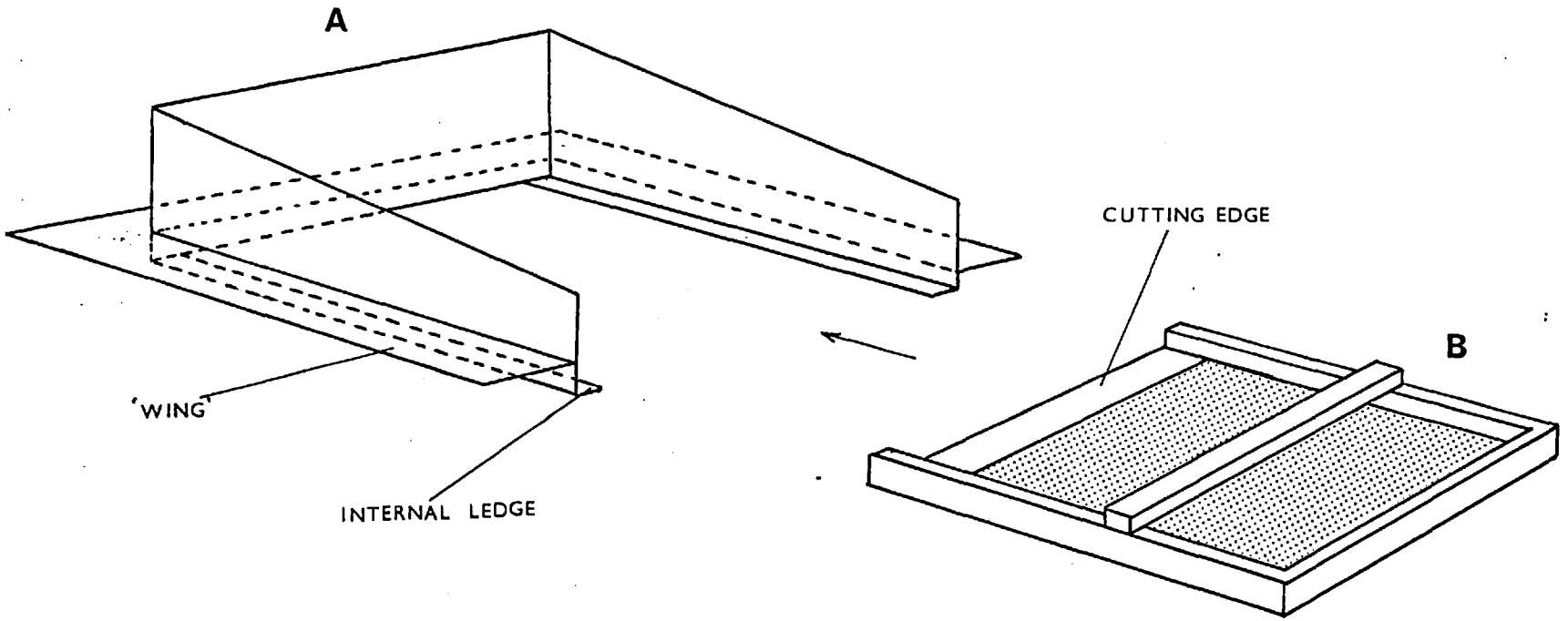


Fig. 10. The sampling frame for collecting leaf samples from the delta surface sediments. The frame A was positioned in the sediment so that the 'wings' were level with the sediment surface. The sieve quadrat B was then pushed into the frame so that the cutting edge ran along the internal ledge of A. When B was then lifted out of A, and the sediment carefully washed through the sieve, the retained leaves were removed and taken back to the laboratory.

macroremains behind. These were then carefully removed from the sieve, returned to the laboratory in polythene bags, and stored in 5% aqueous formaldehyde until required for examination. Plate 2 shows the sampling frame in position on the delta sediment.

Analysis of the leaf remains

After being washed free of formaldehyde solution, the leaves were separated into those that were whole and those that were fragments. The criterion for this division was defined thus:

A leaf was considered to be whole if it was thought to have at least 80% of the area of its lamina present and not less than 80% of its margin intact.

A count was then made of the whole leaves and fragments of each species, and the area of all individuals measured to the nearest 0.25 cm^2 using a gridded perspex overlay. If any fragment proved difficult to identify, the cuticle was prepared by oxidizing the tissues in 20% aqueous chromium trioxide for 12 hours at room temperature. The cuticle was then washed with water, stained in 1% aqueous safranin, and mounted in glycerine jelly, before being identified by comparison with a reference collection of cuticles. The resulting data were subsequently analysed using the multivariate statistical techniques described in Chapter 15.

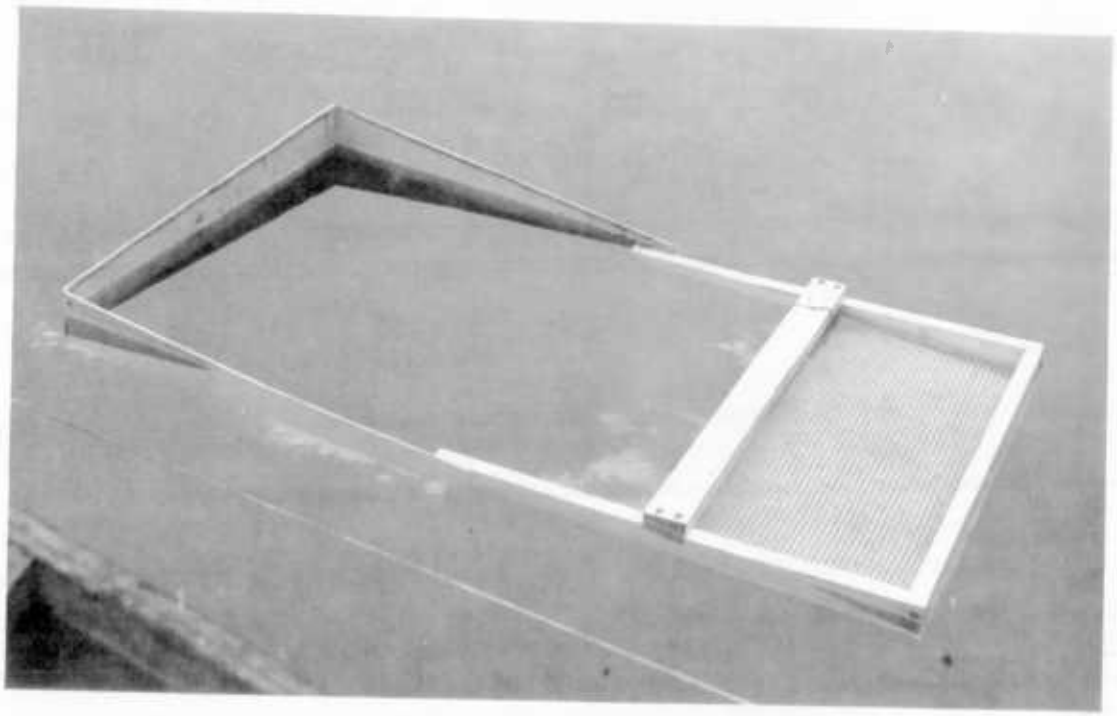


PLATE 2. The leaf sampling frame in position in the delta sediment. The sieve quadrat is shown positioned ready to be pushed into the frame.

INVESTIGATION OF THE THREE DIMENSIONAL STRUCTURE OF THE SILWOOD DELTA

The three dimensional nature of the deposit was investigated by taking a 5 x 4 matrix of 7.5 cm diameter cores in the positions shown in Fig. 11. The corer used was modified from the design published by Livingstone (1955). Various authors have suggested a variety of modifications to Livingstone's original design (Vallentyne, 1955, Rowley and Dahl, 1956, Brown, 1956, Cushing and Wright, 1965), but all use the piston to extract the core. The design described here utilizes a flexible polythene liner and the core may be extracted by cutting this open.

A 2 m length of cylindrical plastic pipe served as the core barrel. This material, which was of light weight, and durable, proved ideal for this type of coring. An externally threaded brass ferrule was fixed to the outer surface of the pipe, 5 cm from the end, with an epoxy resin glue. A brass cutting head screwed on to the ferrule so that an internal brass lip closed on to the end of the pipe forming a flush seal (Fig. 12). The cutting surface of the bit was serrated to aid in penetrating organic debris. A tubular '1000' grade polythene liner was then inserted into the core barrel. The end of the liner was tasselated, bent back over the end of the core barrel, and taped to the external surface of the plastic pipe below the brass furrule. When the cutting bit was then screwed on to the core barrel a tight flush fit was made with the liner. The operation of the corer was then similar to the procedure described in Livingstone (1955).

To facilitate safe working on the delta, a floating drilling 'rig' was constructed, and this is shown in Plate 3. After positioning

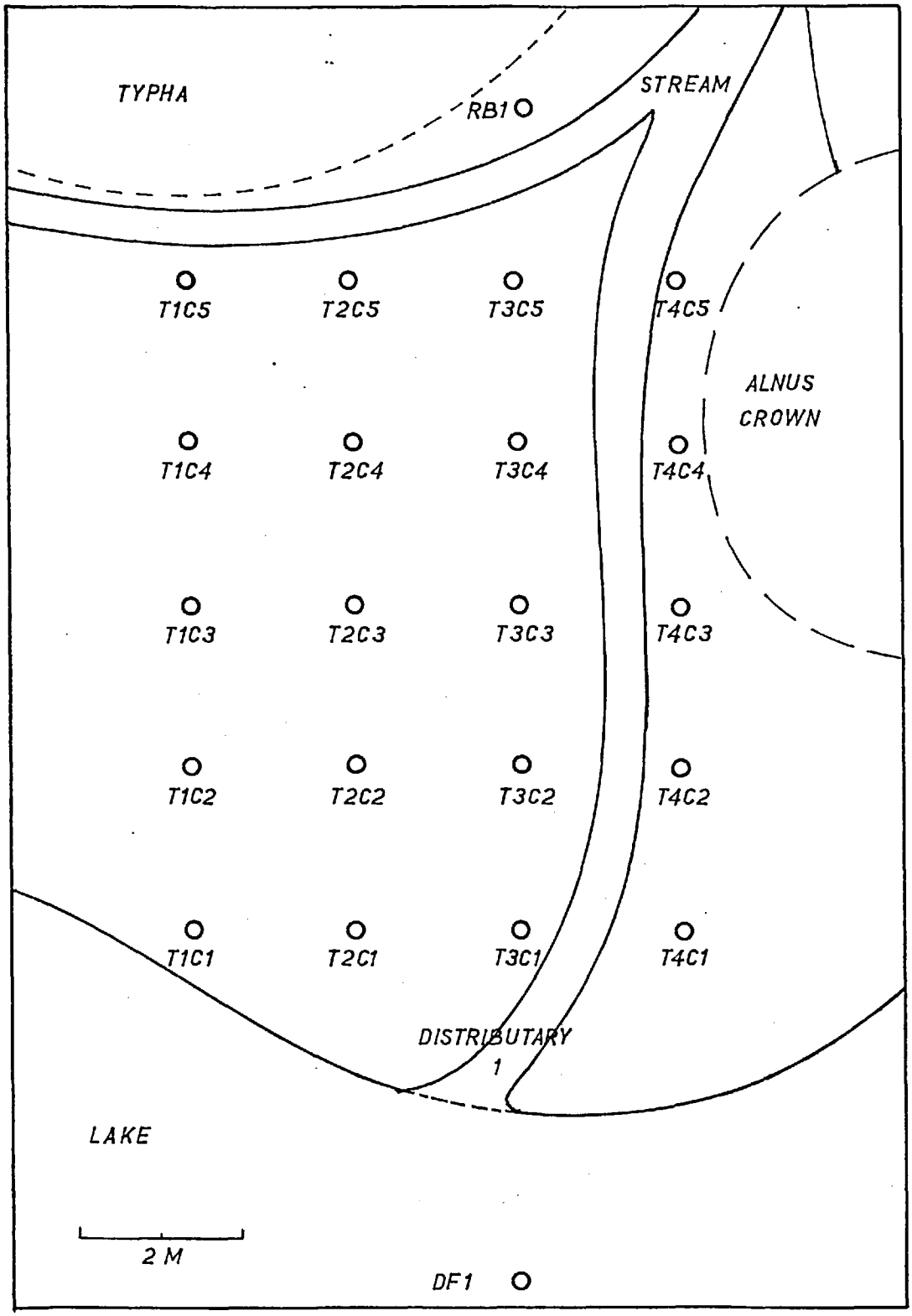


Fig. 11. Positions of the cores in relation to the delta.

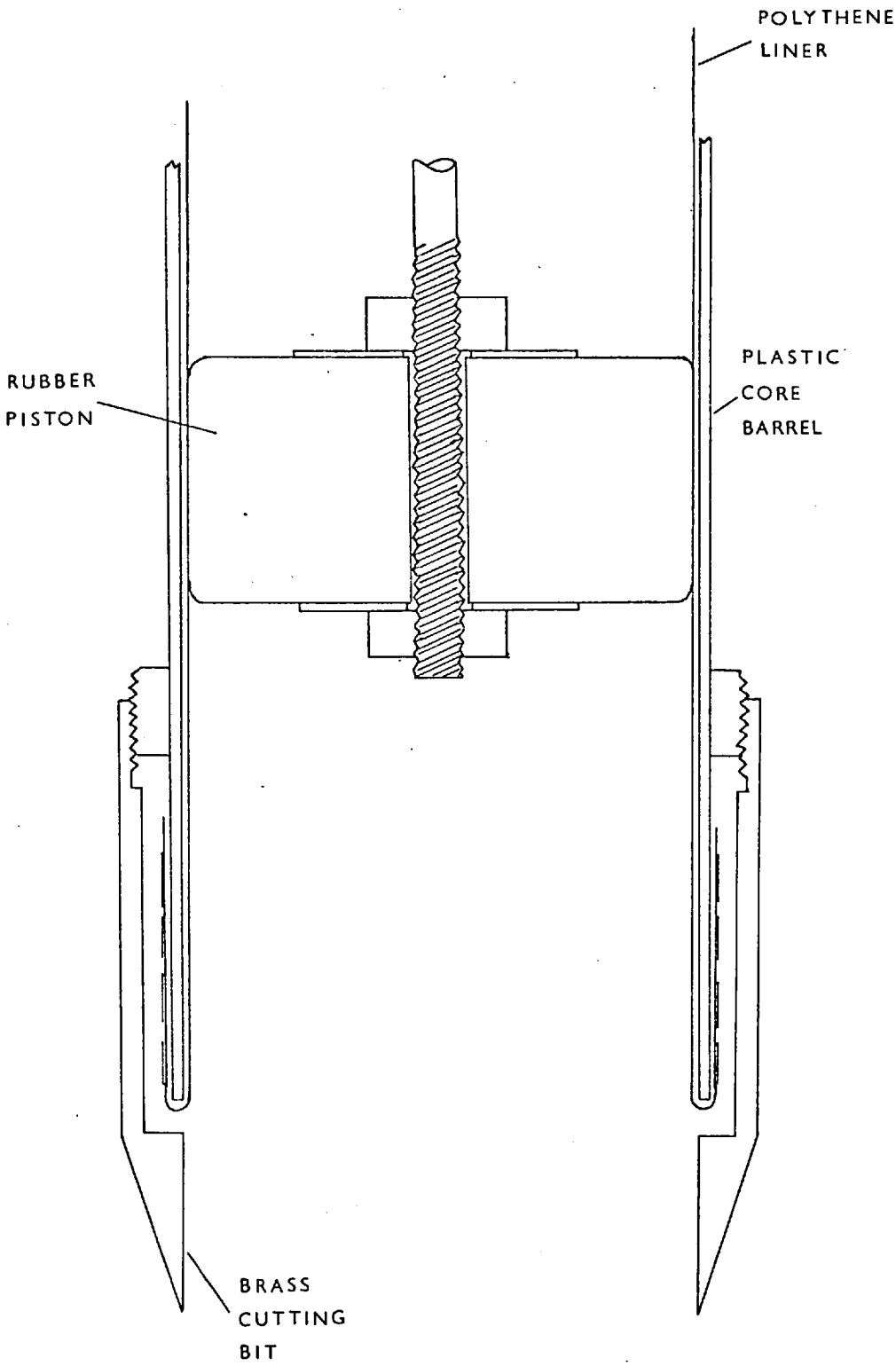


Fig. 12. Corer assembly (actual size). For a description see text.

the rig on the sediment, the core barrel, with its previously inserted liner, and bit were assembled. The rubber piston (Fig. 12) was positioned at the cutting edge of the bit. The piston was then held in place, in contact with the sediment surface, by means of a rope which passed over a pulley at the top of the rig. The core barrel was then pushed manually into the sediment around the piston such that when the core barrel was full of sediment, the piston was at the top end of the barrel and still level with the sediment surface. The piston was prevented from passing back down the barrel, during extraction of the pipe from the sediment, by clamping the piston rope at the top end of the barrel. The barrel was then extracted from the sediment by means of a yoke, which clamped onto the external surface of the plastic pipe and was attached to a rope passing over a pulley at the top of the rig. As soon as the barrel was extracted from the delta it was laid horizontal, the bit and extracting yoke removed, and the ends of the barrel sealed with rubber bungs. The core was then returned to the laboratory before being examined. In this way not less than 95% recovery of each of the 2 m lengths of cored sediment was obtained.

The core was extracted by pulling on the plastic liner after it had been untaped from the end of the barrel. The core was extracted from Livingstone's corer by using the piston. However, when numerous gas vesicles exist in the core this procedure may introduce what might be termed secondary compaction. By extracting the core within the liner this problem was avoided. The core was exposed by cutting the liner with a razor blade. A full description of the core was made and samples of sediment removed for X-ray diffraction studies. The positions of included leaves were noted, and, where the leaf material appeared concentrated, sections of the core were carefully

PLATE 3. Cores of the delta deposits were taken as shown above. The unconsolidated nature of the sediment allowed the core barrel to be driven into the deposits by hand. For a full description of the coring procedure refer to text.

removed for further study.

Originally it was planned to quantitatively sample these core sections, but this proved impossible in the time available. However, the leaves and fragments were carefully removed from the sediment by washing, and a subjective examination undertaken.

Diagrams of the cores are presented in Figs. 72-76, and these are accompanied by a description of both leaf and sediment characteristics.

pH and Eh measurements were carried out, by Dr P. Bush of Imperial College, on freshly extracted cores in the field. After removal of the core from the barrel, the core was retained in the polythene liner. Holes were cut in the liner and the pH/Eh electrode was rapidly inserted into the sediment. The results are shown in table 4.

Approximately 10 g samples of sediment were taken at 0.2 m depth intervals and weighed in aluminium boats of known weight. The sediment was then dried at 80°C to constant weight. The dried sediment was then digested in concentrated nitric acid and the iron content of the digests measured using atomic absorbtion spectrophotometry. The analyses were carried out by Mr B. Hough. Having obtained the iron content of the sediment, the weight loss on drying was then corrected for oxidation of the iron by assuming that no ferric iron was present at the start of the drying, and that total oxidation took place. The corrected water loss on drying, as well as the iron content, is shown in table 4.

POST DEPOSITIONAL CHANGES IN THE ELEMENTAL COMPOSITION OF LEAVES

During fossilization changes take place that alter the elemental composition of plant macroremains from what it was at death. The period of most rapid change undoubtedly takes place during the first year after entry into the depositional environment, and the changes that take place during this time may well play a part in determining which leaves will be preserved, and in what form they will be represented, in the fossil deposit.

To study these changes samples of leaves were placed in nylon cages, as previously described for the degradation experiment, and exposed to both lake and stream environments. After 1, 2, 4, 6 and 8 months degradation, five leaves of each of Alnus, Betula, Fagus, Quercus and Salix cinerea were removed from the cages and returned as rapidly as possible to the laboratory. The leaves were then treated as outlined in the flow diagram (Fig. 13), and as follows:

A. A rectangular (approx. 7 mm x 10 mm) piece of interveinal lamina was cut from the unwashed leaf using scissors. (These facilitated cutting the leaf with the minimum of contamination to either epidermal surface.)

B. The leaf segment was then mounted vertically in a groove that had been cut in an aluminium stub (flat headed rivets were used as stubs) and the two halves of the head of the stub squeezed together to grip the leaf. Two small nicks were made in the leaf, approximately 1 mm above the surface of the stub, to facilitate fracturing in the desired position.

C. The rivet and leaf were then plunged into 'Arcton 12' held at its melting point of -155°C in a bath of liquid nitrogen at -196°C. With the aid of stainless steel forceps the leaf was fractured parallel to the stub surface.

Fig. 13. Flow diagram of the X-ray microanalysis procedure.

A A piece of interveinal lamina was cut from a leaf

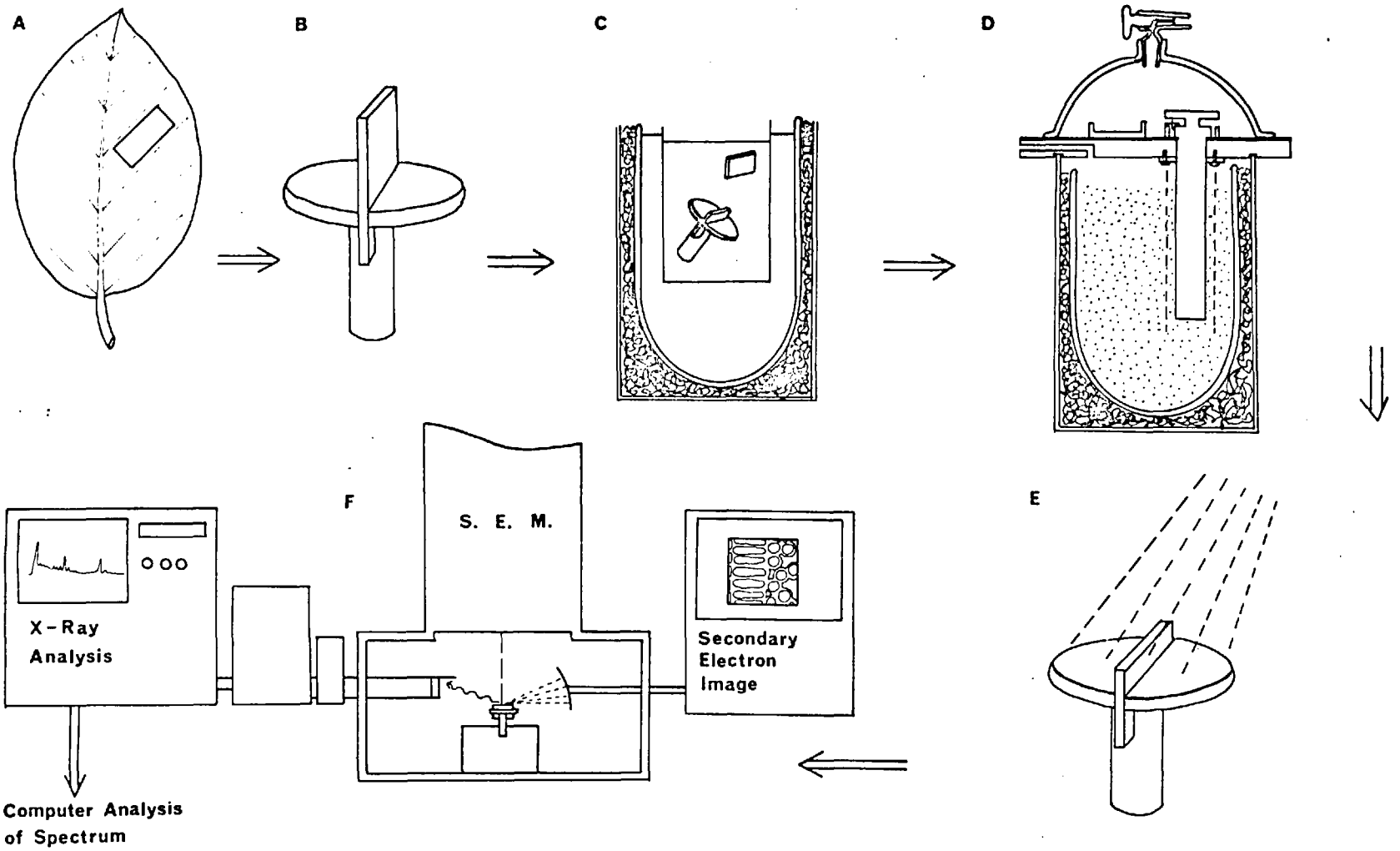
B This was then mounted vertically in an aluminium stub

C The stub and leaf was then quenched in 'Arcton 12' at $-155^{\circ}C$ and the leaf fractured

D The fractured leaf, mounted on the stub, was then freeze dried at $-70^{\circ}C$

E The specimen was then coated with carbon

F The specimen was analysed in the S.E.M.


A
B
C
D
E
F
S. E. M.
X-Ray
Analysis
Secondary
Electron
Image
Computer Analysis
of Spectrum

D. The stub and leaf were then rapidly transferred to the specimen block (previously cooled to -70°C) of a freeze dryer (Spicer, Grant and Muir, 1974) and the leaf was freeze dried at -70°C for 48 hours using phosphorus pentoxide as a desiccant. (Samples from months 1 and 2 employed silica gel as the desiccant).

E. When dry the stub and leaf were transferred from the dryer to a vacuum coating machine and coated with carbon to a thickness of approximately 300 Å.

F. The coated specimen was then examined in a Cambridge Stereoscan MK IIA scanning electron microscope fitted with an Ortec energy dispersive Si/Li X-ray detector. The specimen was aligned with the X-ray detector, as shown in Fig. 14, at a take-off angle of 45°. The specimen was routinely examined under a magnification of x 1000 and by means of the scan rotate and variable raster controls the beam was made to scan, at T.V. rates, a square raster across the palisade and spongy mesophyll cells (Fig.14) It can be seen from Fig. 15 that the volume from which characteristic X-rays are produced is considerably larger than the beam diameter, but by restricting the scanned area to between the epidermal cell layers minimum excitation of the encrusting sediment was achieved.

A counting time of 500 seconds (live time) at a count rate of 1000 cps was used on all analyses, with an accelerating voltage of 20 Kv. The output from the detector was processed by a Northern Econ II multichannel analyser before recording the spectrum data on punched tape for computer analysis.

Computer analyses of the spectra were carried out using a series of interactive Fortran IV programs written by P.R. Grant.

First of all the spectrum was divided up into regions of interest consisting of both peak and background areas. The total area under each peak was calculated and then, by averaging across adjacent background areas, the background under the peak was calculated. From this a peak to background ratio (Pk/Bg) was obtained. A twelfth order polynomial (based on program TREND, Davis, 1973) was then fitted to the total background, caused by the Bremsstrahlung radiation, to obtain an estimate of the total excited mass. Using the fitted background, new peak to background ratios were calculated.

The peak to background ratios were then used to construct a series of graphs (Figs. 100-103) showing comparative changes in element concentration with time and the leaching of elements on entering the stream.

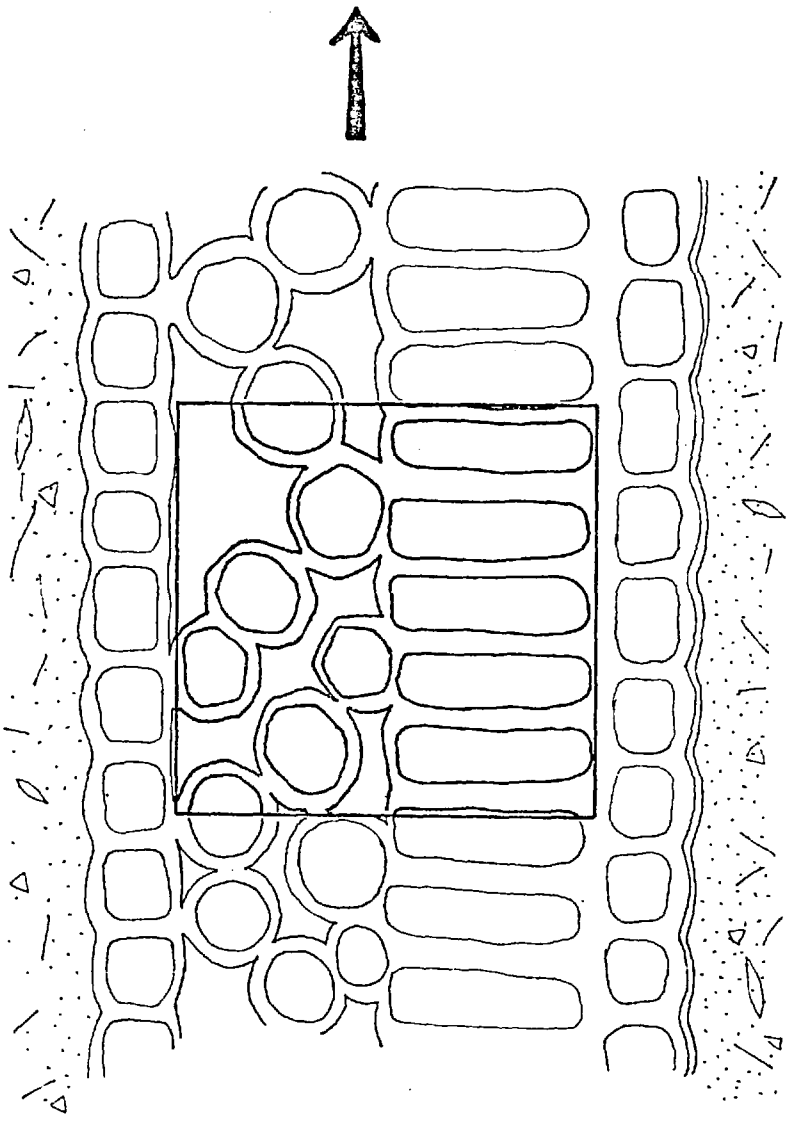


Fig. 14. The area of the fractured leaf section that was analysed is shown diagrammatically above (inside the square). The leaf was orientated to point at the X-ray detector (in the direction of the arrow) at a take-off angle of 45°. In this way excitation of the surface sediment was reduced to a minimum.

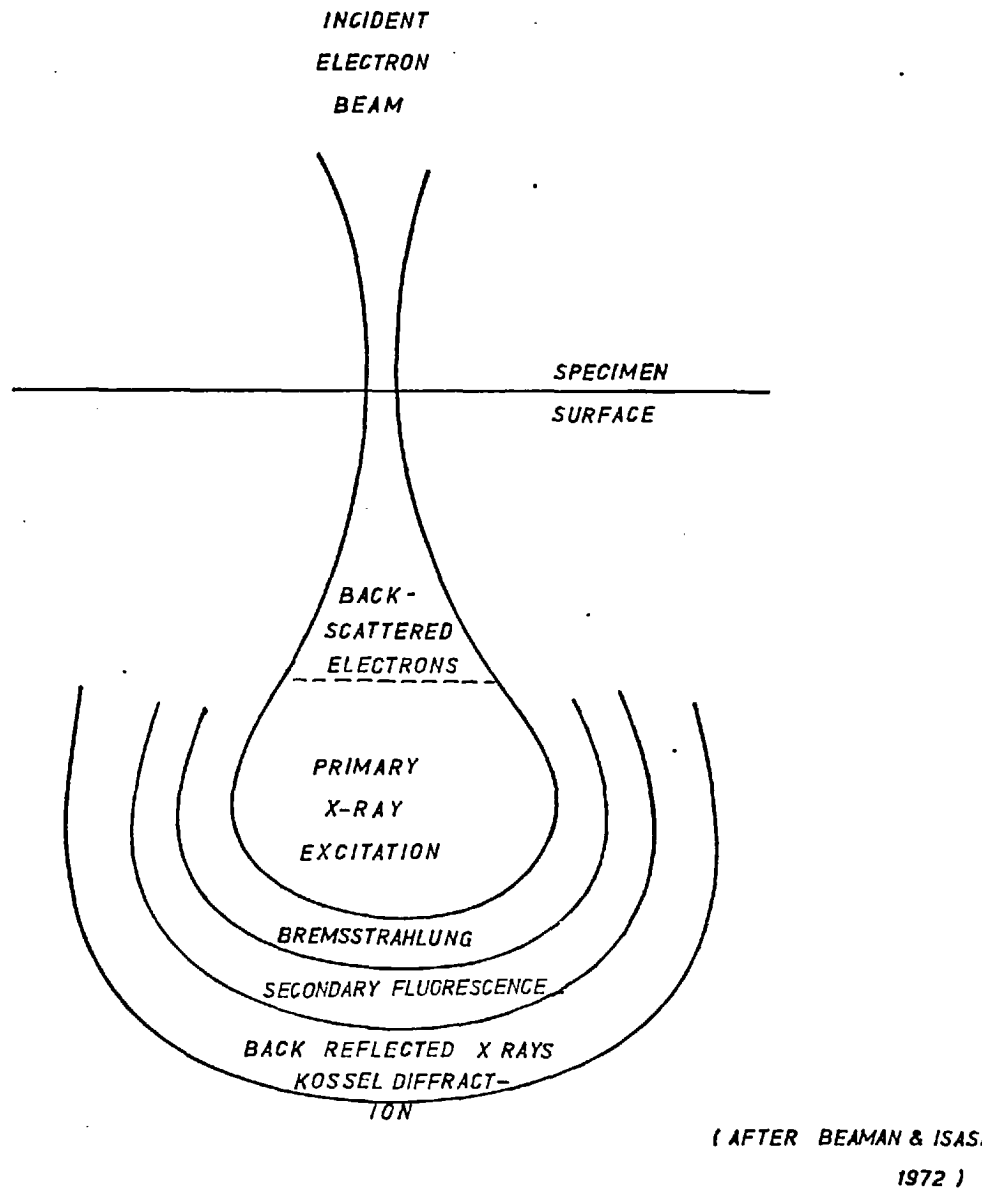
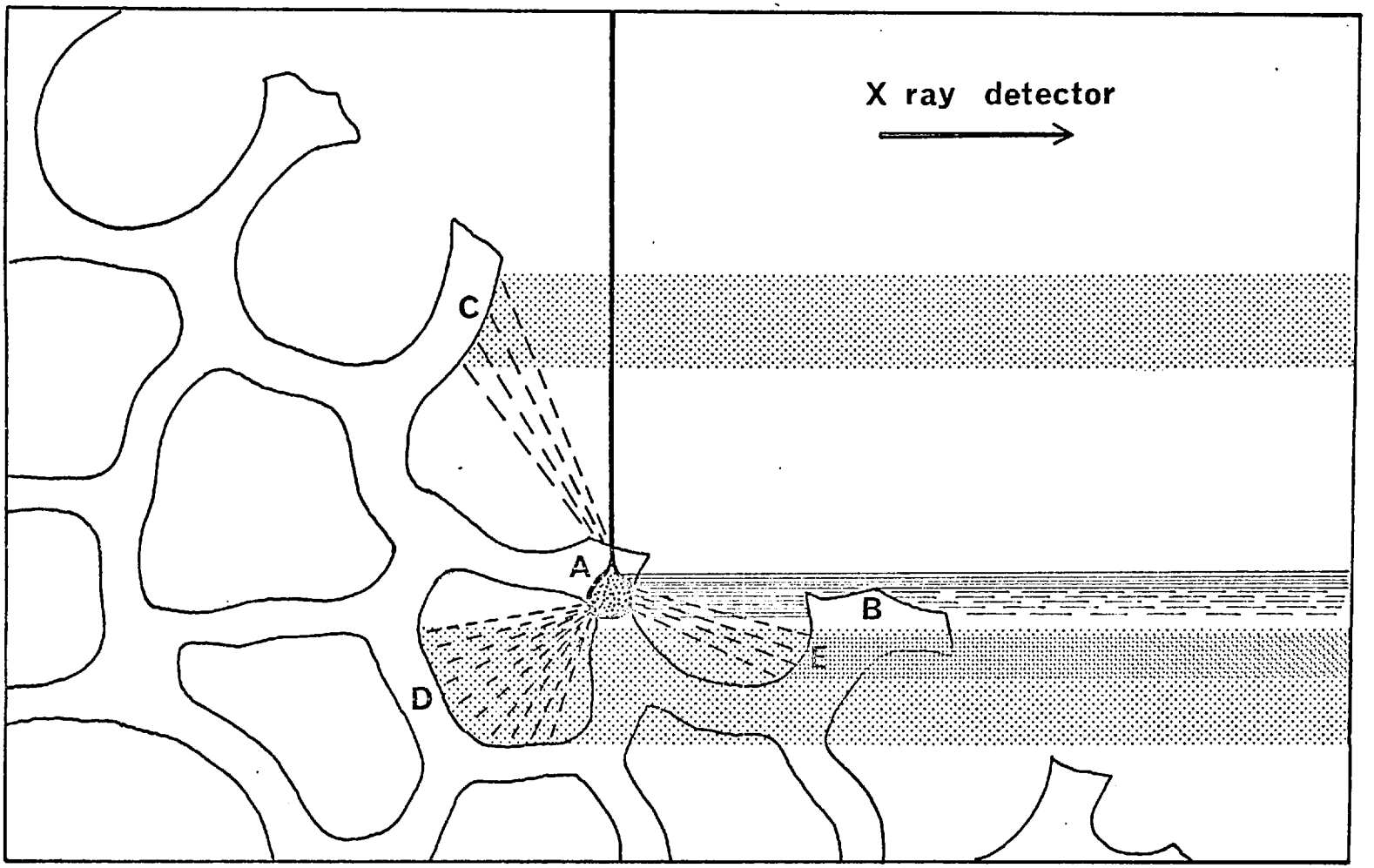


Fig. 15. A schematic representation of the interaction of an electron beam with a solid of moderate to low atomic number.

Fig. 16 The diagram illustrates some of the problems raised by the analysis of rough specimens with internal cavities (e.g. a section of a leaf). The incident electron beam strikes the specimen and generates primary X rays within the exited volume (A). Some of these primary X rays are absorbed by a remote obstruction (B) between the specimen and detector. Backscattered electrons striking other parts of the specimen also produce X rays (C). Some electrons may pass through the specimen and scatter into cavities within the specimen and may have sufficient energy to cause emission of X rays (D&E).



PRIMARY X RAYS

X-RAYS PRODUCED BY BACKSCATTERED ELECTRONS OR ELECTRONS THAT HAVE PASSED THROUGH PART OF THE SPECIMEN.

RESULTS

AND

DISCUSSION

VEGETATION ANALYSIS

Before attempting any comparison between a deposited assemblage of plant remains and the source vegetation it is important to carefully consider in what terms the source vegetation should be described.

The concept of vegetational communities imparts the idea of vegetation being heterogeneous, with each community displaying a greater degree of homogeneity within itself than is exhibited in the whole. In natural vegetation, transitions between communities (ecotones) are rarely well defined, however, and may occupy areas larger in extent than the communities themselves. In spite of this, workers studying pollen dispersal frequently treat vegetation as though it were made up of blocks of uniform composition, and label the blocks according to the apparently dominant species. Each block is then regarded as a distinct pollen source. Delimiting these vegetational areas has usually been a subjective process and the actual parameters likely to control pollen production have not been recorded.

In macrofossil analysis, as well as pollen studies, the 'associational method' of determining the flora has sometimes been used. This method relies on the application of the principal of uniformitarianism taken to its extreme and attempts to 'correct' the palaeoflora, as represented by fossil assemblages, in terms of the species that ought to occur together rather than those that actually do. Wolfe (1969) has discussed the inherent errors of such an approach by using actual examples from the literature. It is reasonable to suppose, indeed it is to be expected, that the species comprising certain types of community have changed with time: that the floristic composition of communities has evolved as well as the individual organism. If studies concerning the distribution of macroremains in present day depositional

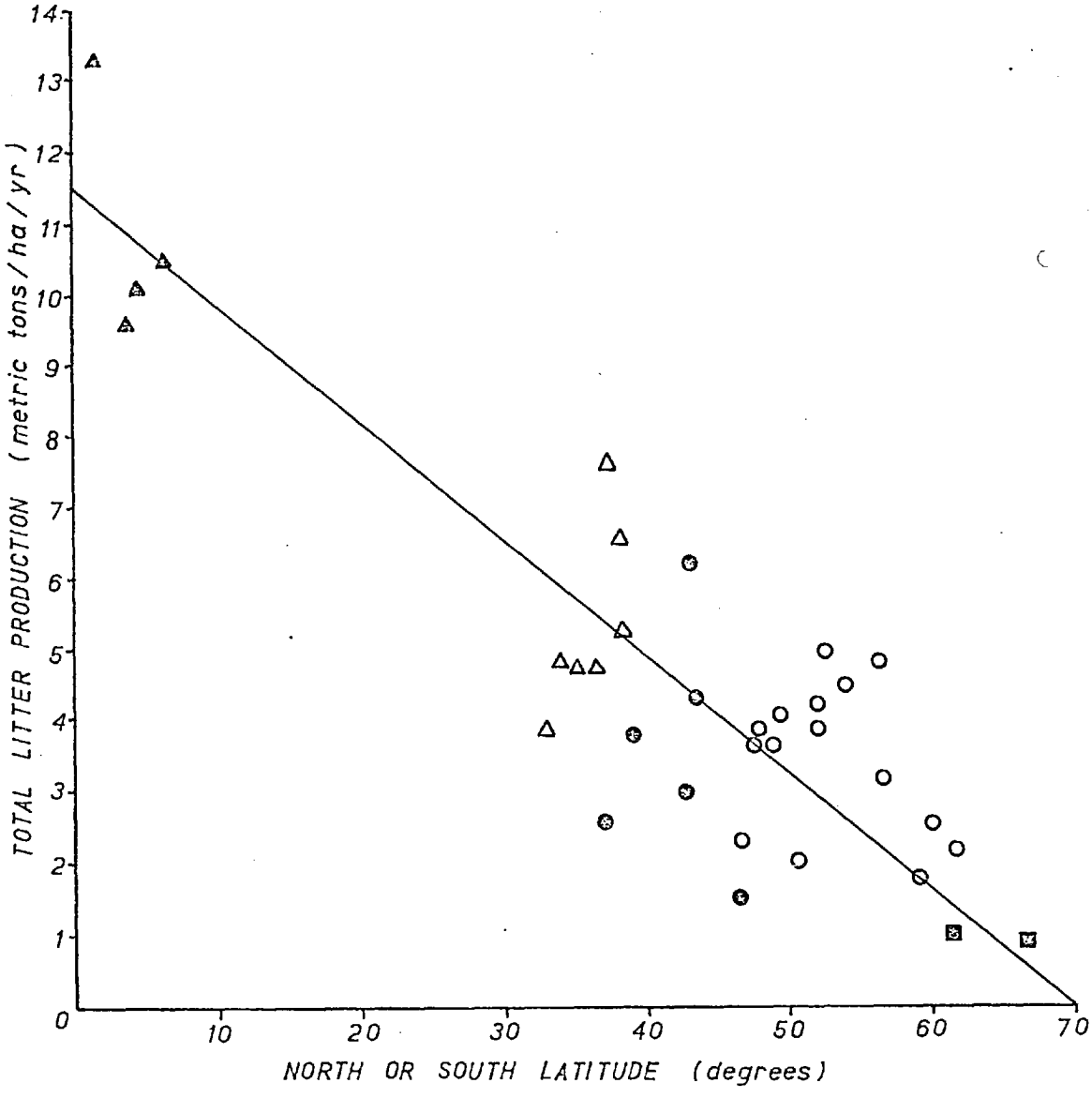


Fig. 17. Annual total forest litter production in relation to latitude. Solid triangles - equatorial, open triangles - warm temperate, solid circles - North American cool temperate, open circles - European cool temperate, squares - Arctic - Alpine. After Bray and Gorham (1964).

environments in relation to the source vegetation are to be in any way applicable to fossil assemblages older than the Quaternary, then more fundamental vegetation measures, other than those relying on species fidelity, are needed.

Although it is dangerous to over simplify vegetation into 'blocked' source areas, such a concept is useful when attempting to reconstruct ancient vegetation. However, the criteria on which divisions of the source vegetation are made, must be related to the type of information likely to be preserved in the potential fossil deposit.

Clearly, as far as macrofossil analysis is concerned, those factors affecting the litter production by the vegetation are important, since a macrofossil assemblage may be thought of as a distorted sample of the vegetations' capacity to produce leaves, fruits, seeds etc. Bray and Gorham (1964) review a series of factors likely to influence the production of litter by a mature stand of forest vegetation and these may be summarized and discussed as follows, bearing in mind that the observations refer to the dry weight of material and not the number of leaves etc:

a) Nature of the trees

Evergreen gymnosperms yield approximately one sixth more total litter annually than angiosperms. The difference in leaf litter alone is 8%. Such differences are only noted, however, when a wide range of sites are considered.

b) Environment

Climate. The effect of latitude is summarized in Fig. 17. If such a pattern existed in the past it is not surprising to find that many fossil assemblages represent tropical, sub tropical or warm

temperate floras, even allowing for high rates of biological degradation under such conditions. The relevance of Fig. 17 to the litter production of ancient vegetation systems is, however, difficult to evaluate. Clearly, the total productivity of a plant community is dependent on the solar energy input, and therefore might be expected to be related to latitude, but this relationship may be radically affected by climatic conditions which, it is known, have dramatically altered from time to time in the past.

Altitude and Exposure. Although the evidence presented is not conclusive, Bray and Gorham suggest that in mountainous areas there is a tendancy for rainfall and temperature to be optimum for forest growth at intermediate elevations. The implication is that litter production would also be at a maximum under these conditions. The chances that a mountain flora will be preserved are slim, thus effects of this kind on litter production are of limited interest to the palaeoecologist.

It is possible that increasing exposure adversely affects litter production, but the evidence is inconclusive.

Soil factors. The data reviewed by Bray and Gorham suggest that there is a tendancy for litter production to decrease with deterioration in soil quality. This effect is most noticeable when the soil factors are different from those required for optimum growth of a particular species. Krasilov (1969) presents examples of how edaphic factors can powerfully influence the floristic composition of a fossil plant assemblage. He was, however , mainly concerned with the effect of major changes in soil type, but less extreme situations of minor soil differences could also affect the likelihood of some species being represented in the fossil record.

c) Tree density

There is no evidence to suggest that tree litter is affected by the density of individuals providing the canopy is complete, but there does, however, appear to be a distinct correlation between the annual fall of litter and the stand basal area in both gymnosperms and angiosperms. In this respect, Bray and Gorham quote the work of Bonnevie-Svendsen and Gjems (1957). It therefore appears that quantitative analysis of closed canopy vegetation using density measures may lead to misleading community classifications from the point of view of the relevance to any derived macrofossil assemblages.

d) Time

Seasonal. As would be expected the pattern of litter fall varies with seasonality of the climate. In equatorial forests fall is more or less continuous throughout the year, but with slight variations due to such climatic fluctuations as wet and dry seasons. In temperate latitudes, of course, most species show a peak in litter production at certain times of the year, most coinciding in the autumn.

Annual variation. The total litter fall may differ greatly from year to year, thus if any meaningful litter estimates are to be achieved, the measurements must be taken over several years. Such a study was therefore necessarily outside the scope of this present work, although litter fall directly on to the lake was intercepted by water traps in order to estimate the relative proportions of species entering the lake by direct aerial transport.

Variations in any of the above factors that affect some species more than others within a community will necessarily affect the chances of those species entering a fossil deposit. In a sense, the deposit 'sees' the source vegetation in terms of the litter productivity of

the various component species. It is worth noting, however, that large portions of the source vegetation are never represented in this way. The herbaceous plants of the understorey (which may comprise up to 28% of the total litter as in young stands of Robinia pseudacacia (Auten, 1941), are rarely represented in the deposited assemblage (Table 3).

The impracticality of undertaking long-term litter measurements from the vegetation of the Silwood drainage basin forced the employment of alternative techniques.

In such vegetation as surrounds Silwood Lake, where there are areas of both open and closed canopies and trees of mixed age, tree density measures are clearly inappropriate. Cover, as defined as the proportion of ground occupied by a perpendicular projection on to it of the aerial parts of individuals of the species under consideration (Greig-Smith, 1964, p.5), would be a more suitable measure since it is more directly related to litter production, but estimating this would be difficult to justify within the scope of the present study.

The measurement of crown cover, i.e. the measurement of the area of horizontal ground surface occupied by a vertical projection on to it of the crown of a tree, was adopted as a compromise that offered a rapid estimate of species abundance that was more or less related to litter productivity. The only portion of the total litter production that has a high probability of being transported by wind any distance to the depositional site, is that produced by the topmost parts of the crown. Here leaves are exposed to sufficiently high wind energies to transport them significant horizontal distances. The only instance in the Silwood environment where the majority of the total litter production from a group of trees could possibly form the input to a depositional environment, is in the case of stream or lakeside

trees. Here the leaves falling into the water are likely to represent a more or less unbiased sample of the woodland litter.

In a closed canopy situation only the very tops of the trees, those parts of the crowns visible from the air, will experience high wind energies and hence have leaves transported over long distances by wind. In open vegetation all parts of the crown will experience sufficiently high wind energies to transport leaf litter, but here again leaves that are most likely to travel significant distances will probably come from the upper parts of the crown.

The crown area, as projected perpendicularly onto the ground does not, of course, represent the actual area of the crown's surface exposed to the wind. If the shape of the crown appoximates to a sphere, then the projected crown area is roughly one quarter of the actual crown surface area. From the above argument the litter source may be restricted to the upper hemisphere of the crown so that the projected area now approximates to a half of the actual area. In closed canopies this difference between the two areas becomes even less since only the topmost portion of each crown is exposed. The leaf density varies throughout each crown, of course, and the distribution is dependent on both species and habit.

It has been assumed so far that those leaves transported by wind originate from the outer surface of the crown. Whether this assumption is justified is open to question since no relevant data is available. What is clear, however, is that on the basis of crown cover, as defined earlier, the error in estimating the size of the source for wind transport is likely to be greater for open vegetation than for woodlands with a closed canopy. This is the opposite of what might at first be assumed.

One way of correcting the crown areas to more closely approximate

to leaf litter production, might be by weighting the crown cover areas by the appropriate leaf area indices. The leaf area index is defined as the total surface area of leaf material of the species under consideration occurring above a unit area of ground surface. If the mean leaf area is known for a species then an estimate of the number of leaves produced by a unit of vegetation may be deduced. The relationship with dry weight, which is the form in which most litter studies are presented, may be similarly calculated. However, as pointed out earlier, only litter produced in the upper parts of the crowns has a chance of being transported to the depositional site by wind.

Discussion of the relationship between crown areas, as viewed from the air, and leaf deposition on the delta

By referring to tables 1 and 2, a direct comparison may be made between the vegetation and the leaves caught in the delta traps. It is immediately obvious that the local species are grossly over-represented. Alnus and Salix, with some Quercus and Betula, form the most local species, and of these, Alnus is the most abundant species bordering the lake, hence its extremely high leaf count from the delta traps. Salix, however, by comparison, is under-represented in the traps. This is undoubtedly due to the filtering action of the Typha bed, bearing in mind that Salix cinerea rarely attains a height in excess of 4 m on the delta. As one would expect, the more distant species, Fagus, Aesculus and Crataegus, are under-represented. Quercus, although occurring more abundantly some distance away from the delta, is a component of the local vegetation. Like Betula, most of this species occurs behind the Alnus on the S.E. lake shore. Thus, once again, considerable filtering by lakeside vegetation reduces

TABLE 1. This table summarizes the vegetation distribution with respect to the delta. Circles were drawn on Fig. 2 with radii representing 50, 100, 150, 200, 250, 300, 350 and 400 m from the centre of the delta. These circles are designated 1-8 in the table. The areas of all the crowns of the various species occurring in the torus between each circle and the next were measured using a 1 mm grid and the percentage species composition was calculated. The total area of the species occurring within the complete circles of successively increasing size is then given as the cumulative percentage composition. Thus the cumulative percentage composition of circle 8 represents a summary of the whole area around the lake.

TABLE 1

	CIRCLE	ALNUS	BETULA	FAGUS	QUERCUS	SALIX C.	SALIX A.	ILEX	AESC-ULUS	CRAT-AEGUS	ACER	FRAXI-NUS	CASTA-NEA
PERCENT	1	51	8		9	32	1						
	2	34	18	2	13	32				1			
	3	25	34	3	10	24			1	2	1		
	4	24	34	6	20	5			4	4	4	1	
	5	18	25	17	26	6		3		2	3	1	
	6	12	28	9	27	8		3	8	2	2		5
	7	11	51	3	17	15		2					1
	8	8	18	31	22				6		9		6
CUMULATIVE PERCENT	1	51	8		9	32	1						
	2	37	16	2	13	32	.			1			
	3	30	26	3	11	27	.		1	1	1		
	4	28	30	4	15	18	.		2	2	2	1	
	5	25	28	7	17	15	.	1	1	2	2	1	
	6	23	28	7	19	14	.	1	2	1	2	1	1
	7	22	31	7	18	14	.	1	2	2	2	.	1
	8	21	28	9	19	13	.	1	2	2	2	.	1

TABLE 2 Numbers of leaves deposited in the delta traps between 12 September 1973 and 14 November 1973

TRAP NO.*	ALNUS	BETULA	FAGUS	QUERCUS	SALIX C.	NUPHAR
1	60	9		5	8	
2	40	4		5	2	
3	49	3		2	4	
4	36	4	3	1		
5	13	1		1	2	
6	10	1	5	2	4	2**
7	3	1	1	3	6	
8	6	1			1	
9	8		1	1		
10	9	7		2	3	
11	13		1	1		
12	23		4	5		
13	65	1	2			
14	86	4		1	1	
15	121	6	7	18		
TOTALS	542	42	24	47	31	2
% OF TOTAL	79	6	3	7	5	-

* See Fig. 3

** Probably transported by water fowl since both pieces bore beak marks and the trap was apparently undisturbed.

TABLE 3

	ALNUS	BETULA	FAGUS	QUERCUS	SALIX C.	ILEX
No. of Fragments	1315	272.	320	559	482	165
No. of Whole Lvs.	722	187	175	69	413	5
Total No. † of Remains	2037	459	495	628	895	170
Frag. No. / Whole No.	1.82	1.45	1.83	8.10	1.17	33.00
Frag. No. / Total No. %	65	59	65	89	54	97
Total* Frag. Area	7561.5	623.5	768.5	826.5	882.0	218.0
Total* Whl. Lf. Area	11573.5	1317.0	2181.5	1053.0	1800.5	30.5
Total* Area	19135.0	1940.5	2950.0	1879.5	2682.5	248.5
%Frag./Whole Area	65	47	35	78	49	715
%Frag./Total Area	40	32	26	44	33	88
Mean Whl. Lf. Area*	15.94	8.10	12.39	15.40	4.36	6.10
S.D. Whl. Lf. Area	10.27	10.21	6.52	8.78	4.37	4.08
Mean* Frag. Area	5.75	2.29	2.40	1.48	1.83	1.32
% Total No. Whole Lvs.	45	11	11	4	26	1
% Total No. Remains	41	9	10	13	18	3
% Total Area of Remains	63	6	10	6	9	1

* Measured in cm^2 † < 2 % UNIDENTIFIED

Summary statistics of the plant remains collected from within the top two

TABLE 3 (CONTINUED)

AESCULUS	ACER	CRATAEGUS	TYPHA	NUPHAR	SALIX A.	TOTALS
23	7	4	185	31	20	3383
9	-	4	-	-	14	1598
32	7	8	185	31	34	4981
2.56	-	1.00	-	-	1.43	2.12
59	100	50	100	100	59	68
232.5	10.5	10.0	321.5	235.0	84.5	11774.0
309.5	-	15.0	-	-	143.5	18424.0
542.0	10.5	25.0	321.5	235.0	228.0	30198.0
75	-	67	-	-	59	64
43	100	40	100	100	37	39
25.79	-	3.75	-	-	10.25	-
20.71	-	3.01	-	-	5.38	-
10.11	1.50	2.50	1.74	7.58	4.23	-
1	-	1	-	-	1	-
1	1	1	4	1	1	-
2	1	1	1	1	1	-

centimetres of delta sediment at the positions shown in Fig. 9.

the probability of representation in the delta sediments.

If table 1 is now compared with table 3, the summary statistics of leaves recovered from the delta sediments, a similar picture emerges. The species percentage representation as based on the number of whole leaves of the different taxa collected from the sediment, shows a closer resemblance to the proportion of the species in the source vegetation, but the over-representation of Alnus is still present. Those species that are extra-local, but grow close to the stream, e.g. Fagus and Quercus are now much less under-represented than those with a wider distribution, e.g. Betula. The proportion of Salix whole leaves in the delta sediments is considerably higher than those arriving on the delta by wind transport, thus it may be concluded that most of the Salix leaves represented in the delta were transported by the stream.

It is obvious that no clear relationship exists between the leaves deposited in the delta and the vegetation as measured by the projected crown area. Indeed it is most unlikely, when one considers the large numbers of variables involved, that a direct relationship can ever be found. The use of proportions to assess the relative representations of the taxa creates its own problems since being a closed system, a departure from a direct relationship exhibited by one species necessarily affects the others. Failure to derive direct relationship between the source vegetation and the deposited assemblage in terms of species proportionality does not preclude the use of alternative approaches to the problem. If it is not possible to deduce how much of a plant was growing in the past, it may yet be possible to determine where it was growing and thereby discover palaeocommunity relationships.

WIND TRANSPORT

The importance of wind transport in the dispersal of fruits and seeds has long been recognized (Ridley, 1930), and in recent years attempts have been made to investigate differential pollen dispersal as an aid to the interpretation of pollen diagrams (Tauber, 1965, 1967). While a number of the concepts described for pollen dispersal may be equally well applied to the transport of macroscopic plant remains, the dispersal of leaves has attracted little attention.

Although leaves cannot be expected to be transported long distances by wind, different species may vary in the distance to which their leaves may be carried, and thus a significantly distorted picture of the source vegetation may be presented by an allochthanous assemblage. The preliminary investigations described here into the possible causes of differential leaf dispersal were carried out in conjunction with Dr D.K. Ferguson.

For the purposes of experimentation wind transport may be divided into a vertical and a horizontal component both of which operate simultaneously in nature. The experiments to investigate the effect of leaf size, shape, and weight on dispersal were carried out using artificial leaves, the parameters of which could be controlled within narrow limits. 'Leaves' made of air mail paper (0.0030 g/cm^2), cartridge paper (0.0123 g/cm^2) and card (0.0346 g/cm^2) were used. These materials were cut into circles, equilateral triangles and two rhombic shapes of length to breadth ratios of 1.45:1 and 6.90:1 respectively. In most experiments two sizes of each shape were used; 11 cm^2 and 44 cm^2. Some additional measurements using units of 22 cm^2 were also made.

The time taken for the units (which were released with their

flat surfaces horizontal) to fall a vertical distance of 3.18 m in still air was recorded and the results are shown in Fig. 18 .

Once on the ground leaves may be blown laterally and an attempt to investigate this aspect of dispersal was made by blowing leaves, both artificial and natural, along a plane flat surface using a PHYWE fan. This fan was moved from side to side over a distance of 3 m for a period of 1 minute so that all the leaves were blown evenly. Although the air flow from this fan was extremely turbulent, and by no means uniform, the relative dispersal of the 'leaves' could be determined and the results are shown in Figs. 19(a and b).

The results of these experiments suggest the following generalizations.

Shape

It was observed that while falling through still air shapes with axes of unequal length tended to rotate about the longest axis. This affected the flight so as generally to increase the length of time a leaf remained in the air as well as the ground dispersion. These differences are insignificant, however, when compared with those due to variations in weight.

Flat shapes blown horizontally along the ground were distributed laterally by a combination of saltation and rolling; the greatest lateral dispersion being found with circular shapes which tended to roll. When the flat shapes were folded the distance transported increased for a given wind speed but imbrication caused a pronounced positive skewness to be given to the histogram (Fig. 19(b)). A similar effect was noticed for curled Fagus leaves.

Size

The rate of vertical fall in still air appears to be little affected by size alone, except that the small shapes of the heavier materials had a tendancy to be more stable in the air and generally remained horizontal in flight after being released in that position. This was also seen to occur with the larger size of the heaviest material. The effect of this phenomenon was to reduce ground dispersion.

No significant difference in lateral ground dispersion could be attributed to size.

Weight

Variations in falling rates in still air appear to be largely determined by differences in weight per unit area more than any other single factor. Shapes made from the heaviest material showed little variation between sizes, while air mail paper shapes showed more. This may be due to the relative increase in importance of size at low weight levels. As would be expected, shapes with a greater weight per unit area had the shortest falling time while the lightest shapes took correspondingly longer. The relationship, however, does not appear to be linear (Fig. 18).

Variations in lateral movements of dispersed units under the influence of horizontal winds also appear to be largely determined by weight per unit area. At all three weight levels used in the experiment the lateral dispersion of each group was normally distributed over the same number of distance classes irrespective of distance travelled. However, increasing weight caused a progressive shift in the mean of the distributions towards the wind source (Fig. 19(a)).

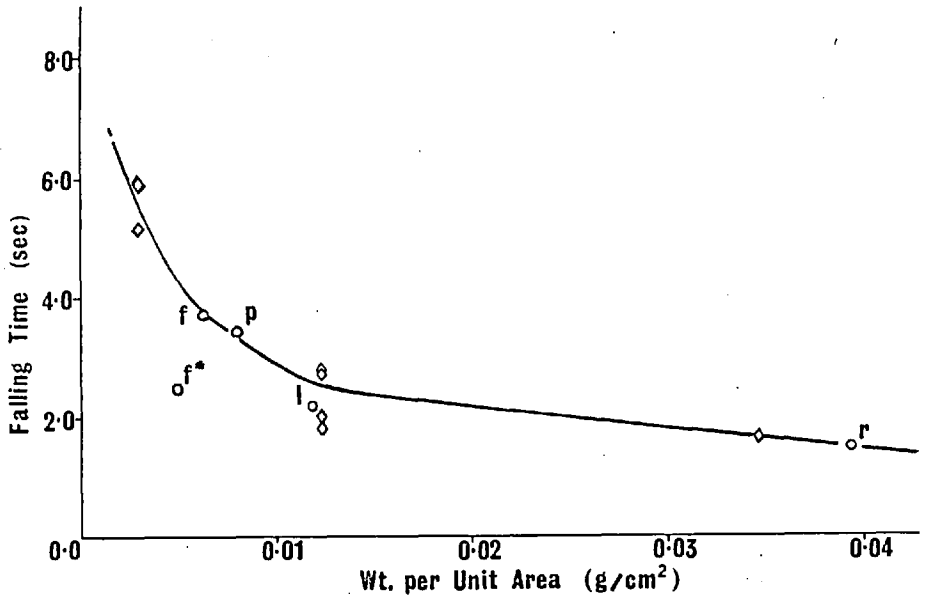


Fig. 18. The falling times of leaves (both paper and natural) to fall a distance of 3.18 m in still air plotted against their weight per unit area. Rhombic shapes represent paper leaves and the circles natural leaves. r - denotes Rhododendron, l - Laurus nobilis L., p - Platanus X hispanica Muenchh, f - Fagus sylvatica L. (flat), f* - F. sylvatica curled.

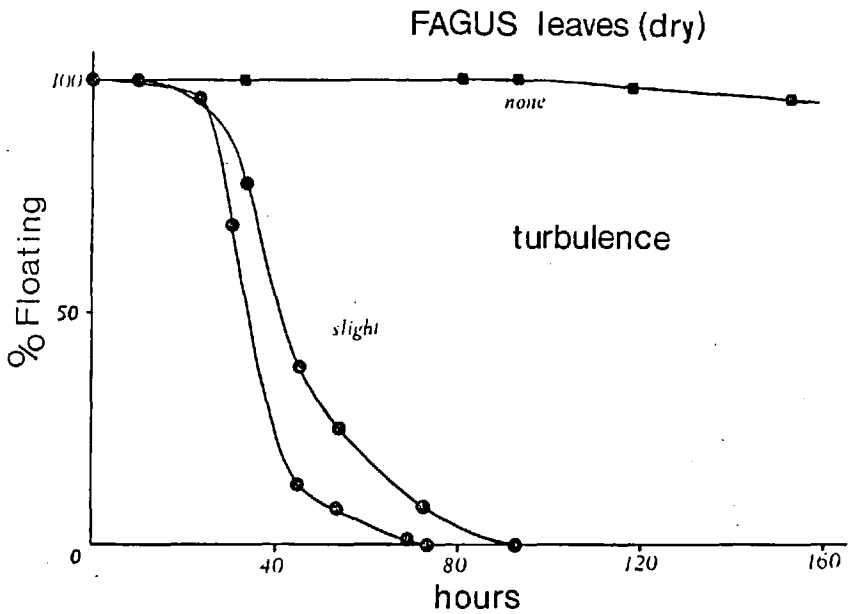
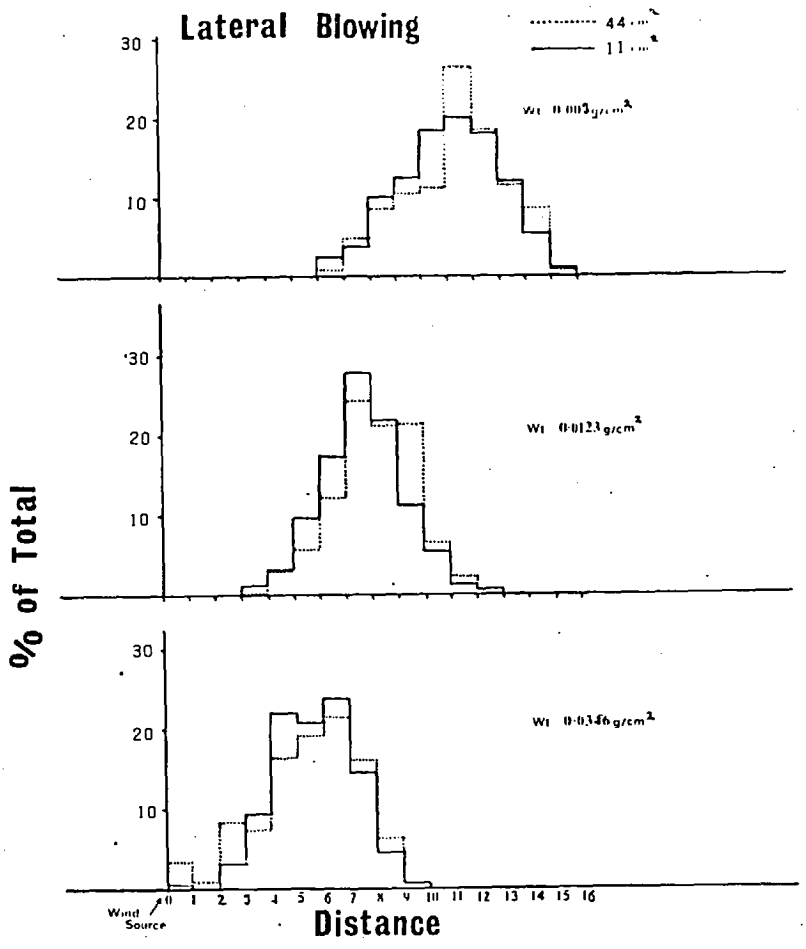
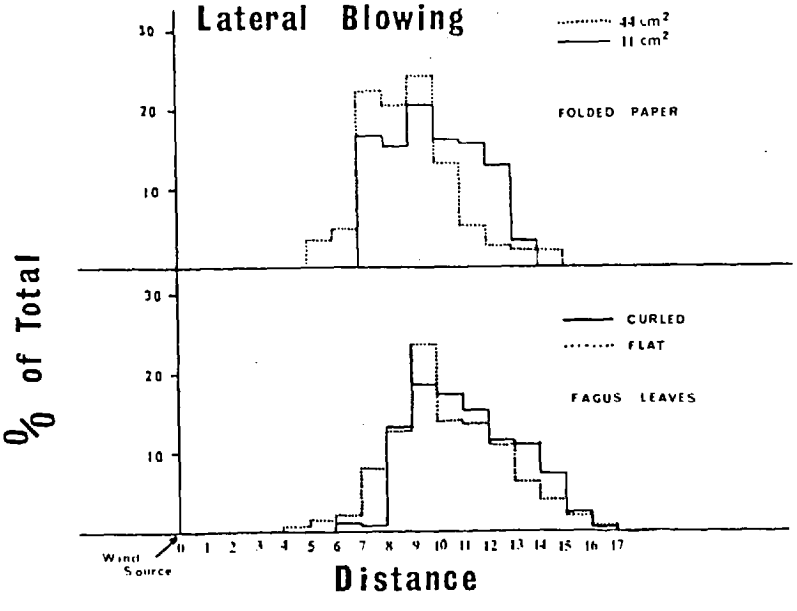


Fig. 20. Dried Fagus sylvatica leaves floating times.

Fig. 19(a). The lateral blowing of flat rhombic paper leaves (length to breadth ratio 1.45:1) along a plane flat surface. The effect of weight per unit area is clearly seen. The horizontal distance the leaves will travel will clearly depend on the wind strength, thus arbitrary distance classes were used.

Fig. 19(b). The horizontal distance travelled by folded paper (0.0123 g/cm^2) as compared with that of both flat and curled Fagus leaves under the influence of a given wind speed. The curled Fagus leaves appeared to be blown fractionally further than flat leaves, but imbrication caused a pronounced positive skewness to be given to the histogram.


Lateral Blowing
44 cm²
11 cm²
30
20
10
Wt 0·0123 g/cm²
Wt 0·0346 g/cm²
% of Total
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Wind Source
Distance


Lateral Blowing
44 cm²
11 cm²
FOLDED PAPER
CURLED
FLAT
FAGUS LEAVES
30
20
10
% of Total
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Wind Source
Distance

The artificial paper leaves used in the above experiments all lacked a petiole, but experiments carried out with dried natural leaves indicate that the effect of the petiole is negligible except where it accounts for a substantial part of the total weight of the leaf or is exceptionally long.

Leaf size sorting at Silwood

As well as the variation in leaf weight per unit area and size between species, considerable differences exist between sun and shade leaves within a single species, e.g. Fagus sylvatica. The leaves at the top of the crown of many trees tend to be considerably smaller and with a greater weight per unit area than those lower down, particularly in a dense forest canopy. In spite of these differences the top leaves have a greater chance of wider dispersal because they are exposed to higher wind energies than those within the canopy or trunk space. Thus the majority of leaves of the distant species, such as Fagus sylvatica, caught in the delta surface traps (Fig. 22) were small sun leaves and not, as might be expected from the laboratory experiments, leaves with a smaller weight per unit area.

The difference in mean leaf area between leaves trapped on the delta, and those from the stream in the mixed woodland above cascade bridge, was extremely large for Fagus sylvatica and was shown to be significant at the 1 per cent probability level (Fig. 22). It cannot be argued that the delta sample was restricted to that from one group of Fagus trees that might bear only small leaves since the absence of any strong prevailing wind direction during the sampling period suggests that the sample was as representative of the surrounding vegetation as was possible (Fig. 21). By way of contrast Fig. 23 shows a comparison of Alnus leaves from the delta traps with a sample

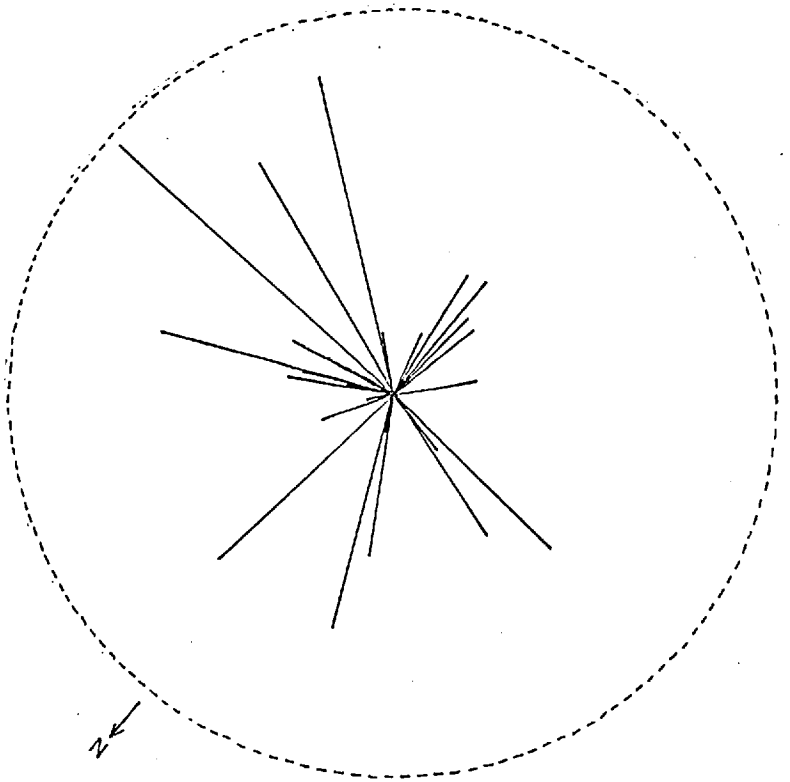


Fig. 21. Mean Wind Directions for July to December 1973. R is related to the closeness of clustering of the component angles of wind direction (weighted for speed (knots)) and is defined as the distance from the centre of a unit circle (circle with a radius of 1).

WEEK	MEAN DIRECTION	R	MEAN ANGLE OF DEVIATION
July 4-10	282 (deg)	.10	76.9 (deg)
11-17	184 "	.14	75.0 "
18-24	275 "	.29	68.0 "
25-31	165 "	.09	77.2 "
Aug 1-17	7 "	.32	66.5 "
8-14	221 "	.03	79.6 "
15-21	31 "	.05	78.8 "
22-28	110 "	.36	64.6 "
Sept 29-4	329 "	.22	71.5 "
5-11	93 "	.49	57.8 "
12-18	179 "	.20	72.4 "
19-25	129 "	.07	77.9 "
Oct 26-2	333 "	.05	78.9 "
3-9	30 "	.10	76.8 "
10-16	172 "	.19	72.7 "
17-23	325 "	.31	67.1 "
24-30	78 "	.15	74.4 "
Nov 31-6	64 "	.12	75.7 "
7-13	60 "	.14	74.8 "
14-20	192 "	.14	74.8 "
21-27	66 "	.32	66.8 "
Dec 28-4	221 "	.11	76.0 "
5-11	82 "	.07	77.8 "
12-18	287 "	.22	71.2 "
19-25	127 "	.43	60.9 "
MEAN	82 "	.03	79.4 "

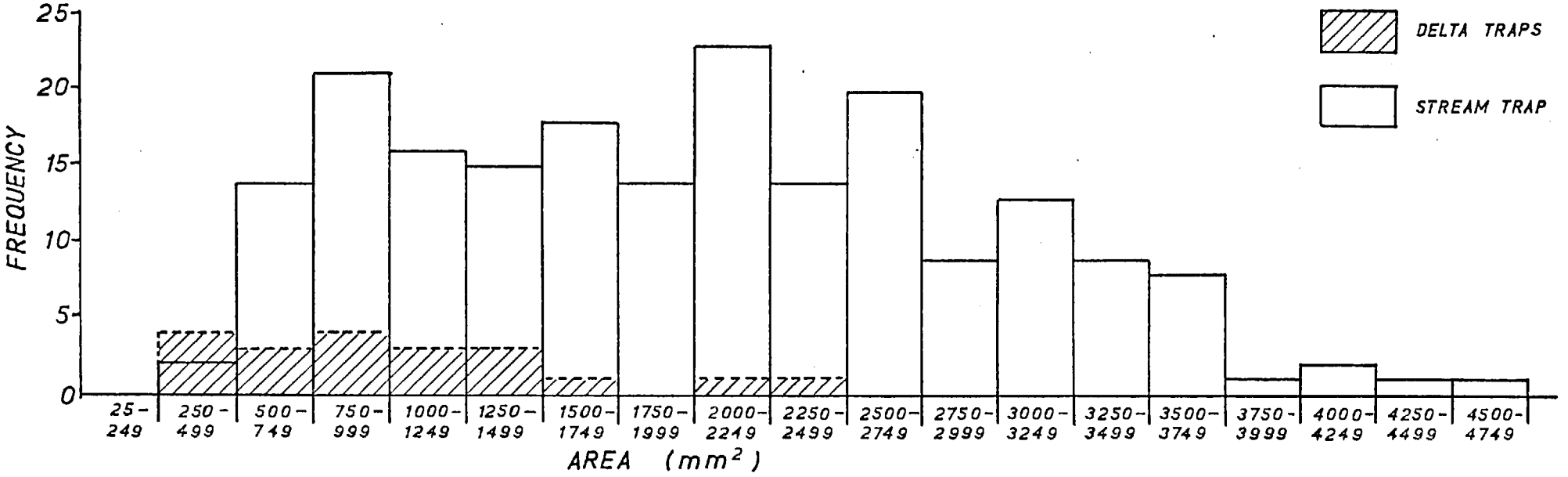
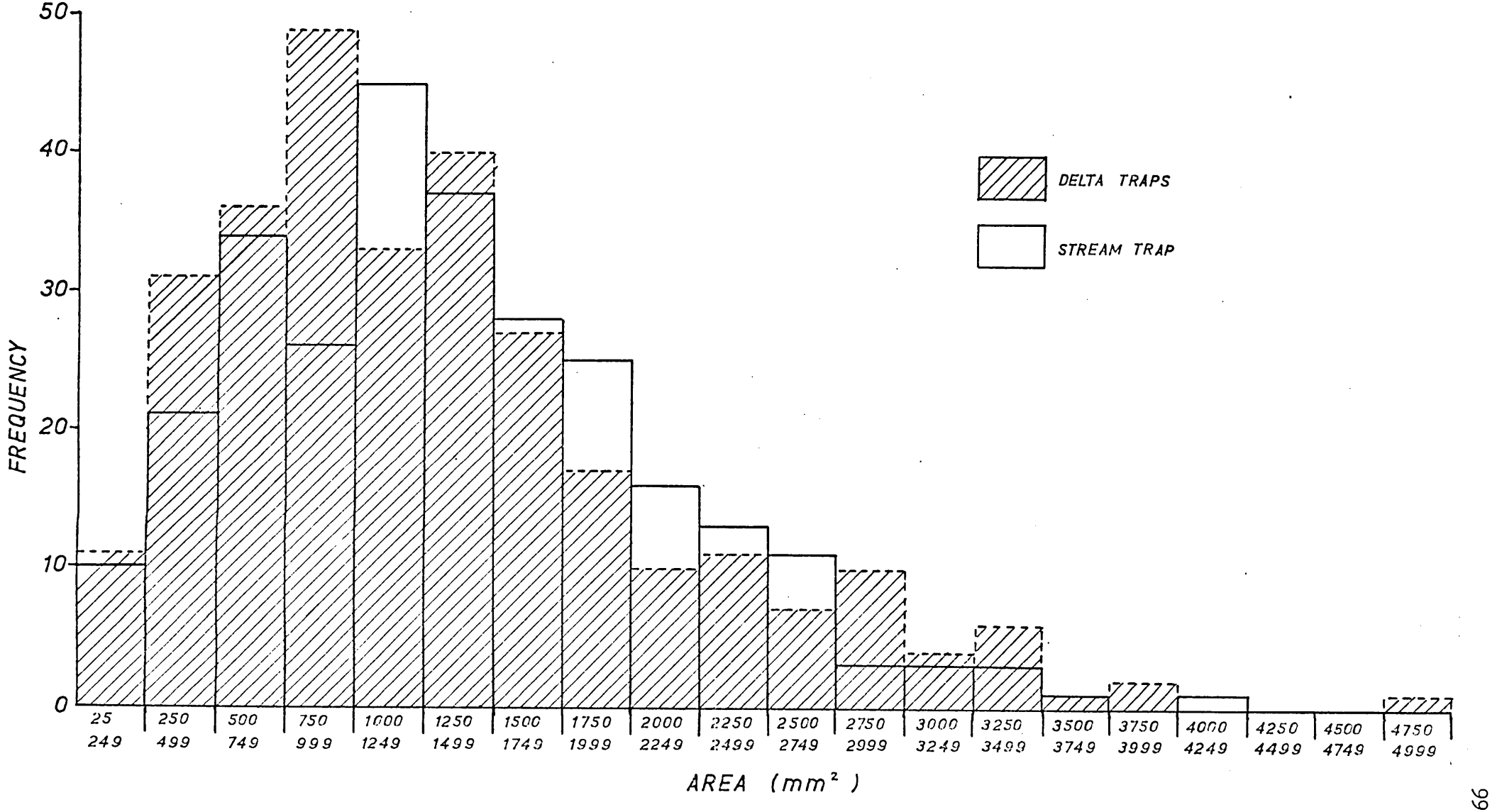


Fig. 22. Size frequency histogram for Fagus sylvatica leaves recovered from both stream and delta traps. The stream trap was positioned in a part of the stream that flowed past a number of mature trees. These trees formed a closed canopy over the stream and the sample may be considered to be representative of litter on the woodland floor. Following the Fisher-Behrens test for two sample comparisons with unequal variances (as described in Campbell, 1967) the null hypothesis that the two populations were equal as regards their means had to be rejected since the observed d = 6.94, which exceeded the published value at the 1% level of significance.

Fig. 23. Size frequency histogram for Alnus glutinosa leaves recovered from both stream and delta traps. The distributions can be seen to be very similar with perhaps a slight positive skewness exhibited by the delta sample. The Fisher-Behrens test showed there was no significant difference in the means (d = 0.56).


50
40
30
20
10
0
FREQUENCY
DELTA TRAPS
STREAM TRAP
25 249
250 499
500 749
750 999
1000 1249
1250 1499
1500 1749
1750 1999
2000 2249
2250 2499
2500 2749
2750 2999
3000 3249
3250 3499
3500 3749
3750 3999
4000 4249
4250 4499
4500 4749
4750 4999
AREA (mm²)

of Alnus leaves from a stream leaf trap. There is no significant difference in the means although a slight skewness to the left is seen in the delta sample. This suggests that even with leaves from local elements of the flora a larger proportion of small leaves enter the lake than are representative of the litter from the surrounding vegetation, although the difference may not be significant.

Palaeoclimatic implications

The representation of at least part of the flora by only the small dense leaves has important consequences for palaeoclimatic interpretations based on fossil deposits.

Dilcher (1973) discusses the correlation of leaf size with climate and demonstrates how both temperature and moisture influence the relationships. The wet tropics are characterized by a high percentage of large leaves; while a change to a drier or cooler climate is accompanied by an increased percentage of small leaves. Wolfe (1971), however, recognized the problems posed by differential selectivity during transport and deposition; "..... large leaves obviously will, in many environments, tend to be fragmented by turbulent currents and hence be under represented. Another problem is that fossil assemblages may contain an over-representation of stream-side plants (MacGinitie, 1953, p.46), and thus stenophyllous plants that typically fall into the low size-classes (Richards, 1952 [1966]) may be over-represented. Such over-representation would yield an analysis indicating a cooler climate ....."

Dilcher (1973) points out that in the clay deposits of Kentucky and Tennessee there are leaves of greatly differing size classes occurring together, and that Wolfe's assumption that the linear or lanceolate leaves, typical of stream sides, are smaller in total area

than those in the forest, is open to question. However, Dilcher's observation that both large and small leaves occur in the Tennessee deposits in no way invalidates Wolfe's argument, since the Tennessee material was undoubtedly laid down under tranquil conditions whereas Wolfe was considering a higher energy, more fluviatile, environment in which the larger leaves would tend to be destroyed. In any case it is impossible to disprove, from such a fossil flora, that over-representation has not taken place.

From observations on Fagus sylvatica leaves deposited in the Silwood stream trap it is clear that leaves entering a small woodland stream are more or less representative of the forest litter. However, in more open waters distant components of the surrounding flora are represented only by the smaller leaves; a result of differential aerial transport. Thus while it is difficult, in the absence of any positive evidence, to agree with Wolfe's assumption that over-representation of small leaves is due to over-representation of stream-side plants, differential aerial transport of leaves from extra local species can bring about a similar effect, resulting in the fossil flora apparently representing a cooler or dryer climate than is actually the case.

Climate, in turn, will affect the dispersal of leaves since high humidity conditions will increase the weight per unit area of the leaves, and, if liquid water is present, their ability to be transported by aerial saltation and rolling will be seriously diminished since they will tend to cling together, and to any substrate, by surface tension forces. This aspect of climatic control over dispersal has been discussed by Ferguson (1971). He has also noted that high humidity will tend to promote a well-developed river system which will take over a certain part of the role played by wind action in dispersal.

Dispersal through the trunk space

Tauber (1967) considered that objects such as pollen passing through the trunk space in a forest will tend to be caught on shrubs next to a clearing. Work carried out by the author with Dr Ferguson (unpublished data) has shown that leaves of Laurus nobilis L. will only be trapped on the windward side of a diffuse obstacle, such as a bush, provided that the wind speed is low (<10 Km/hr). Speeds a little in excess of this create a build up of leaves behind the obstacle (provided that the leaves can pass through the 'mesh' of the obstacle), and at higher speeds this leeward tail increases in length. This is due to the wind energy being dissipated in turbulence behind the obstacle leading to a deposition of the 'suspended' load. Pollen, however, being so much smaller with a much slower settling velocity, is likely to pass through more or less unaffected.

The effect of the deciduous habit

Of all the leaves examined from the Silwood deposits not one could be assigned with certainty to any herbaceous species. The importance of the leaf shedding habits of plants in affecting their chances of representation in the fossil record has been noted by other authors (e.g. Chaney, 1924 and Ferguson, 1971). The lack of the deciduous habit results in the leaves of herbaceous plants withering and disintegrating while still attached to the stem; hence the extreme rarity of herbaceous plants in sedimentary environments. While this is an extreme case many deciduous trees also fail to shed leaves, particularly when juvenile (e.g. Fagus sylvatica and Quercus robur), which must in turn distort the fossil record.

The evergreen species do of course shed their leaves, but usually do so, not in the autumn, but when new growth begins. For example

Ilex aquifolium L. commonly sheds its leaves in the spring. In fact it has been noted by Bray and Gorham (1964) that evergreen gymnosperms, as well as being generally more productive, yield approximately one sixth more total litter annually than angiosperms, though this is not necessarily in the form of leaves. Seasonal shedding of leaves probably greatly affects the dispersal of plant remains especially if the leaf fall from one component of the flora coincides with a rainy season whilst the remainder shed their leaves during the dryer part of the year. Thus the spring fall of Ilex may well lead to a different dispersal pattern to that exhibited by leaves shed in the autumn months.

WATER TRANSPORT

Botanists have long recognized the importance of water in the transport and dispersal of plant remains. An account, by Moseley (1892), of observations on plant debris transported out to sea by the river Ambernoh in New Guinea was quoted, and made famous, by Reid and Chandler (1933). They proposed a similar transport mechanism to explain the occurrence of leaves, fruits and seeds in the London Clay. Berry (1906) observed large 'rafts' of leaves being transported downstream by river waters, while H.N. Ridley, as well as writing an excellent book on plant dispersal (Ridley, 1930), made numerous observations on the transport of plant debris by floods following tropical storms. A number of such reports are brought together in a vivid discussion on the mode of formation of fossil floras by Chandler (1964, pp 4-8).

Leaves transported by wind undergo very little fragmentation, but are only carried comparatively short distances. Thus, fossil assemblages with a high proportion of whole leaves, such as those typical of the Mississippi embayment Eocene floras, probably represent those plants which were growing immediately around the depositonal environment. This, however, may not always be the case as some reports (e.g. Berry, 1906) show.

Rivers may transport leaves over considerable distances (Ridley quotes seven miles for beech leaves) although a high degree of fragmentation by either biological or mechanical agencies is to be expected.

Discussion of leaf floating experiments

H.N. Moseley (1892), while on board H.M.S. Challenger, observed

the transport of plant debris off shore from the mouth of the river Ambernoh, New Guinea, and made the following report:

"The leaves evidently first drop to the bottom, whilst vegetable drift is floating from a shore. Thus as the debris sinks in the sea-water a deposit abounding with leaves, but with few fruits and little or no wood will be formed near shore, whilst the wood and fruits will sink to the bottom further off land."

The powerful effect of differential sorting brought about by differences in the floating times of various plant organs has, therefore, long been recognized.

Preliminary experiments with Fagus sylvatica leaves showed that if only one side of a leaf is wetted, and there is little wave action, such leaves may remain afloat almost indefinitely, buoyed up by surface tension. Conditions such as these are, of course, rare in nature, being only found in small pools within forests with a closed canopy, in which case such transport as there might be is minimal and confined to the limits of the pool. Slow flowing rivers might also have comparatively calm surface waters where a leaf might remain afloat in this manner for some time.

If both surfaces of a leaf are wetted and the leaf is in only slightly turbulent, oxygenated water, significant increases in floating time may arise due to the formation of gas bubbles on the leaf. Using the light beam apparatus (Fig. 5), it was found that this phenomenon also caused previously sunken leaves to float once more. In order to make valid comparisons of floating times between species, by achieving consistent results, it was necessary to agitate the surface waters periodically. Unfortunately, even minimal agitation caused flow currents to be set up in the water which were found to be

of sufficient energy to stir up leaves that had already sunk, but had buoyancies only slightly in excess of neutral. The stirred up leaves frequently interrupted the light beam and gave false readings. For these reasons, the light beam apparatus was found to be only of limited use. The effect of turbulence and air bubble formation is demonstrated in Figs. 20, 24 and 25.

In the turbulent surface waters of a lake or river, however, bubbles might well be knocked off as soon as they had formed, and the sinking of a population of leaves is likely to follow the pattern observed in the majority of laboratory bucket experiments. Figs. 20, 24, 26 and 27 show the results of such experiments and the range of floating times likely to be commonly encountered. Often the sinking pattern resembles the cumulative log-normal distribution curves typical of dosage response.

At first it was considered suitable to analyse such curves using probit analysis. However, the design of the experiments were such that this was inappropriate (Finney, 1970 p.27). If the experiments were redesigned to conform to the form required for probit analysis, i.e. based on successive batches of test leaves, rather than a single batch tested during a continually increasing dosage, such an analysis would be ideal for expressing the differences between species. The concept of the E.D. 50 for instance is eminently suitable for summarizing the sinking of a population of leaves, and by converting the log normal distribution to a straight line, direct comparisons with other species may be made.

It can be readily seen that the vastly differing floating times exhibited by the various species could result in a high degree of species sorting. The wide variations in floating times caused by air bubble formation dependent on the turbulence of surface waters means,

Fig. 24. Results of Alnus glutinosa leaf floating experiment carried out in a bucket with frequent agitation.

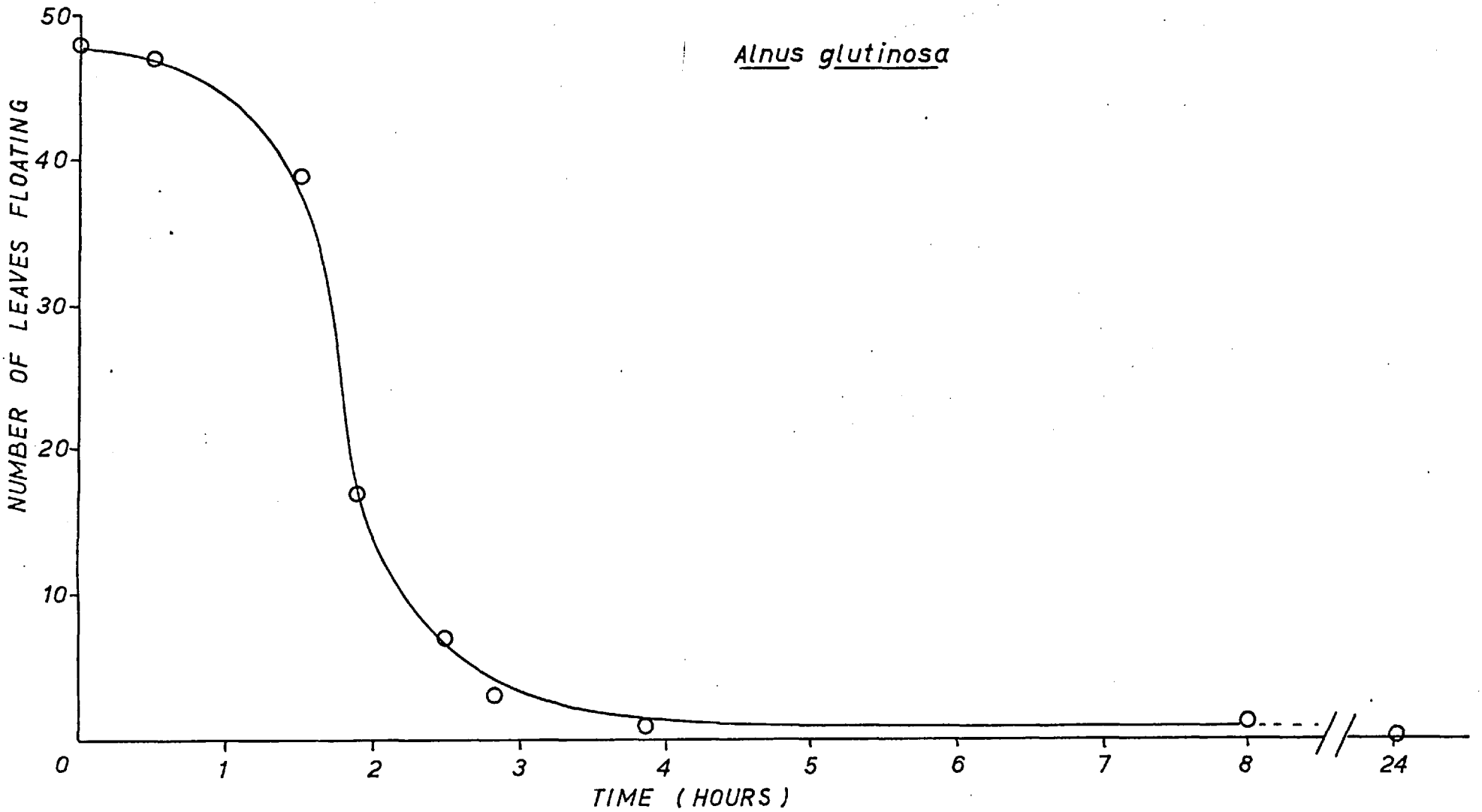


Fig. 25. Alnus glutinosa floating experiment carried out in the light plane apparatus and no agitation.

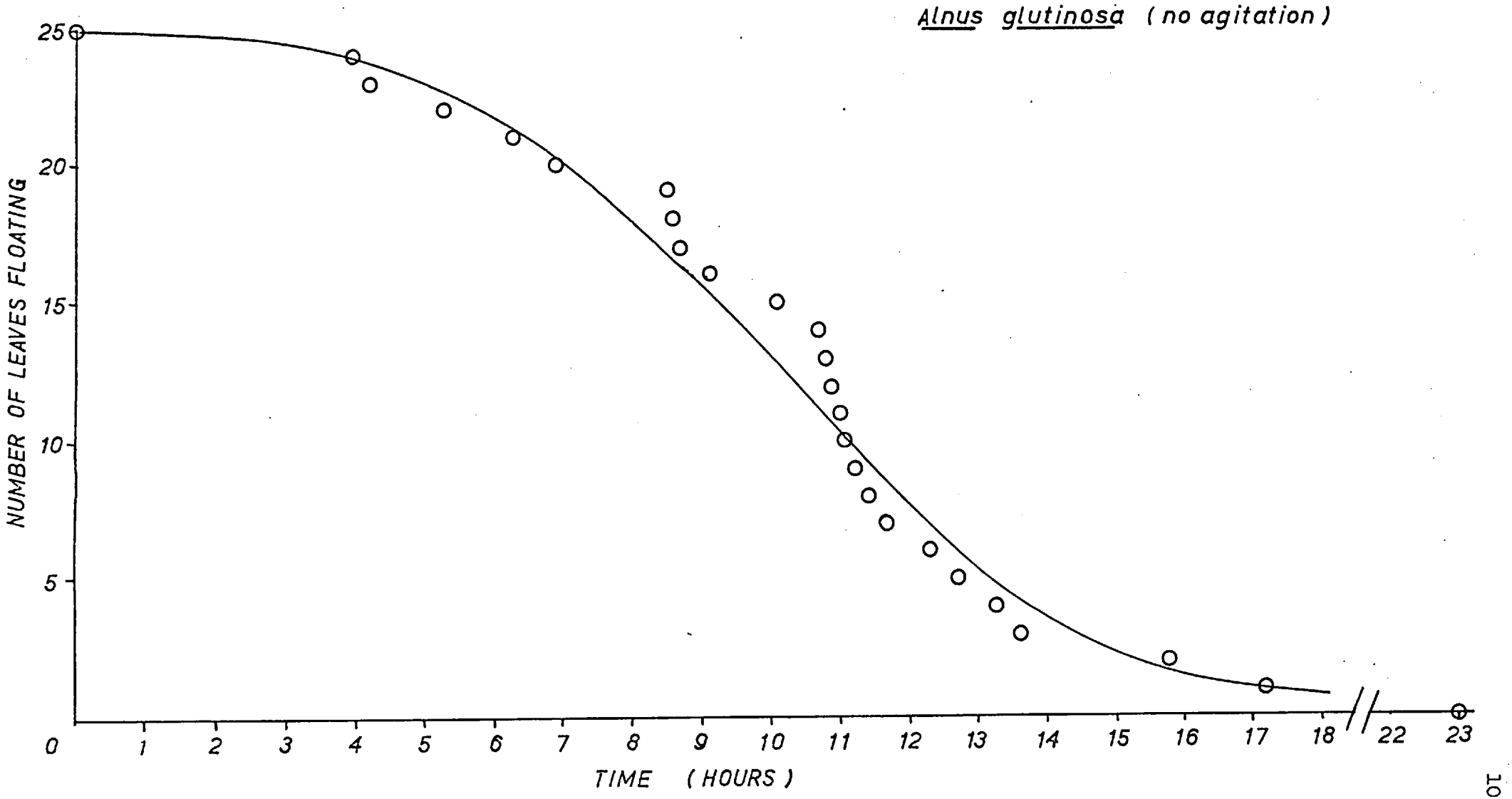


Fig. 26. Floating time experiment with freshly fallen Ilex aquifolium carried out by the 'bucket' method and frequent agitation.

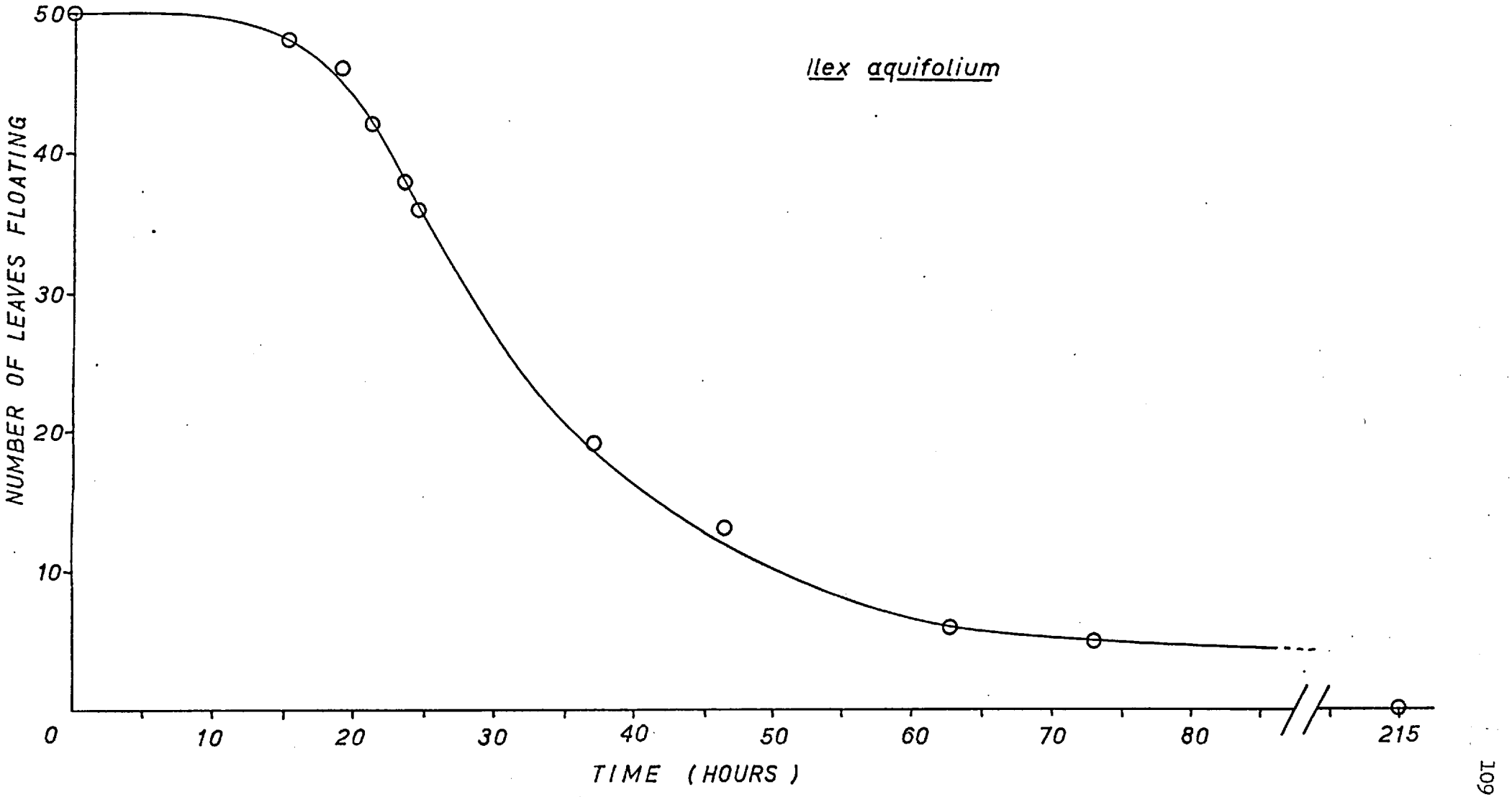
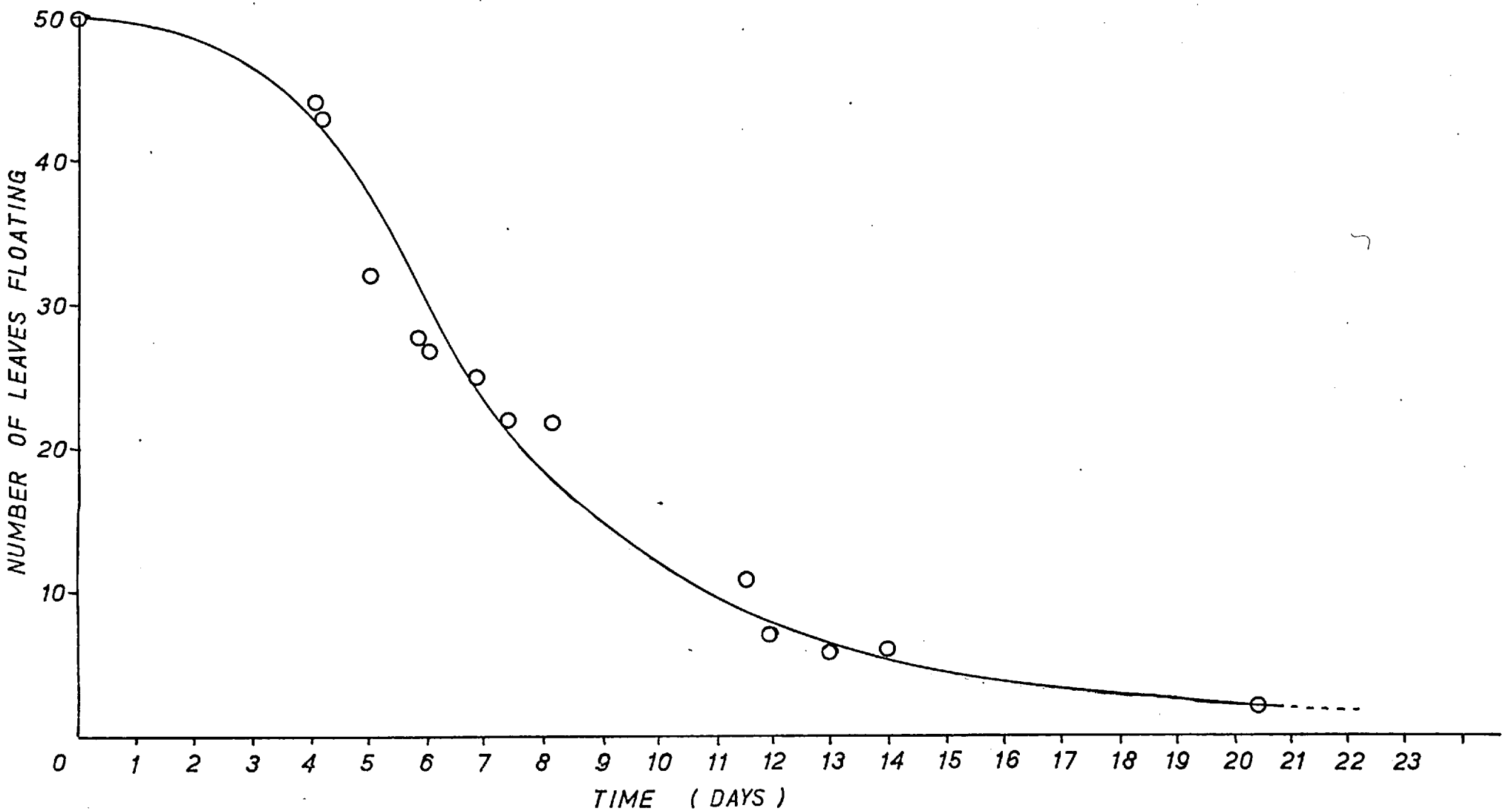


Fig. 27. Floating time experiment with freshly fallen Rhododendron sp. leaves as recorded from a bucket experiment and frequent agitation.



however, that little precision in palaeocomunity reconstruction is likely to be achieved by studying this aspect of dispersal. However, analyses of floating times are important in determining the likelihood of a fossil being represented far from its growing point and therefore the possibility that it may represent a distant source community.

Leaf degradation

Leaf fragmentation and ultimate destruction in the course of water transport is a major factor influencing the representation of a species in the fossil record. It has long been recognized that certain species are more resistant to breakdown than others, but most of the work that has been done, has expressed degradation in terms of weight loss rather than in measures directly applicable to palaeobotanical problems. Weight losses may occur due to leaching of soluble substances, for instance, which do not directly affect that leaf being represented in the fossil record. In the present study, therefore, degradation is presented as a series of figures showing the extent of lamina loss. The amount of leaf material surviving destruction will clearly determine whether or not the species is recognisable in the fossil record.

Petersen and Cummins (1974) carried out their studies of leaf degradation by constructing 10 g. artificial leaf packs of single species (held together with a nylon fastener) and measured the weight loss of the packs over known periods of time in stream environments. The packs were constructed to be similar to the 'stacks' of leaves often observed in streams on the upstream side of obstacles during the autumnal leaf fall. An alternative experimental method is to expose leaves to the degrading environment enclosed within nylon

bags (e.g. Mathews and Kawalczewski, 1965). The latter approach has the advantage that access by degrading organisms may be controlled by the mesh size of the bags. The use of single species, whether in the form of leaf packs or enclosed within nylon bags, may be criticized in that the ecology of the organisms affecting breakdown may be altered by restriction of the food source to one species, and hence breadkown does not proceed as it would do under natural conditions where a number of different species are likely to be present.

In the Silwood study, it was decided to use samples of leaves of mixed species. More or less rigid nylon cages (0.5 cm^2 mesh size) were used in order to allow access to even the largest invertebrate detritivores while at the same time retaining all but the smallest leaf fragments. The rigidity of the cages ensured that the leaves were, to some extent, protected from mechanical breakdown (except of course, that caused by abrasion between themselves). This was desirable since estimates of the mechanical strength of the leaves were to be determined at various times during the experiment. Instead of estimating dry weight loss as a measure of degradation, the outlines of the leaves were recorded. This, of course, only measured breakdown in terms of the visible leaf lamina loss and not internal tissue destruction as might be caused by micro-organisms. However, the amount of the lamina, and, more especially, the area of intact cuticle would ultimately be the criterion that would determine whether species identification in the fossil state would be possible. The degree of breakdown, as affecting the mechanical strength of the leaf, which in turn determines the susceptibility to fragmentation, was also investigated.

The dominant energy source of a small woodland stream is the

allochthonous input (e.g.see Egglishaw, 1964, Cummins et. al., 1972, 1973) and it has been demonstrated that the aquatic insect community has become synchronized to the autumnal input of leaf material (Hynes , 1961), that is to say that emergence, oviposition and eclosion occur just prior to leaf abscission. The type of leaf degradation caused by invertebrate organisms may be classified into that brought about by the activities of large particle feeders, and that produced by small particle feeders (Petersen and Cummins, 1974). The activity of both these groups of organisms may be seen in Figs. 28-43. The large rounded holes are typical of the large particle feeders, while the removal of predominantly interveinal tissue only is the result of the activities of the small particle feeders. The midrib and large secondary veins are seldom damaged, even by the large particle feeders, except when the rest of the lamina is almost completely destroyed (e.g. Fig. 36,stream 4 months). Sometimes attack appears to begin at the margins (e.g. Fig. 37,lake 1 month) but extensive damage to the lamina rapidly takes place so that by the fourth month in the lake environment some leaves are extensively degraded.

It can be seen that the degree of degradation that takes place within a given time interval varies from species to species. Petersen and Cummins (1974) suggest that differential invertebrate destruction of leaves is a function of microbial colonization and conditioning. In this respect, they quote the work of Kaushik (1969) who proposed that selection of leaves for food by invertebrates was probably determined by differential rates of microbial colonization. Early work by soil ecologists indicated that the rate of breakdown of organic matter was related to the type of organism involved in the processing, and the chemical nature of the material, especially the

nitrogen content (Waksman and Tenny, 1927, Waksman, Tenny and Stevens, 1928 and Melin, 1930). Melin (1930) found that within a species there was a direct relationship between the amount of nitrogen in the material and its rate of breakdown. However, between different species this relationship was not so clear as other factors, such as the amount of lignin or antifungal compounds present also affected microbial colonization. Mathews and Kowalezewski (1969), using bags of different mesh sizes, found that although bags with a coarse mesh size (3 mm) had a greater invertebrate fauna, the leaves did not breakdown any more rapidly than in bags with a fine mesh size (0.27 mm). They concluded, therefore, that the majority of losses (dry weight) are due to the activity of microorganisms. They also noted significant increases in the nitrogen content of the leaves, presumably due to the uptake of nitrogen by increasingly large numbers of microorganisms.

The rate of invertebrate leaf degradation is controlled by microbial conditioning, and in turn, the rate of microbial colonization seems to be dependent on the chemical compositon of the leaf. However, as Nykvist (1962) has shown, the chemical composition of leaves can alter markedly within a few hours of entering a stream. He anaerobically leached samples of Alnus glutinosa, Fagus sylvatica and Quercus robur leaves and found that after 24 hours leaching Alnus had lost 12% of its dry weight as soluble organic substances. In contrast, Fagus had only lost 3.8% and Quercus 7%. Water soluble inorganic substances lost after 1 day of leaching amounted to 1.3% dry weight for Alnus, 1.1% for Fagus and 0.9% for Quercus. Most of the inorganic substances were lost after 1 day, since continued leaching did not bring about any significant further losses. Grinding Fagus litter produced an increased loss of 2.4% of the dry weight in the form of water soluble organic substances after 1 day's

leaching. For Quercus the increase was 6% but for Alnus the increase was only 0.2%. For inorganic water soluble substances, grinding gave an increased loss of 0.3% for Fagus, 0.2% for Quercus but no increase for Alnus. The amounts of water soluble organic substances obtained by aerobic leaching were slightly less than those from anaerobic leaching.

Grinding appears to lead to very little increase in the loss of soluble organic substances from Alnus leaves which indicates that all the leachable substances are removed from the intact leaf and therefore leaching is not inhibited by the structure of the leaf. Quercus and Fagus lose less than Alnus, partly because the water soluble organic substances are bound by the leaf structure and are only released when the leaf is extensively damaged. It is known that tannins occur in large amounts in Fagus and Quercus in the insoluble condensed form and that they have antifungal properties (Benoit et. al., 1968, and Williams, 1963). If tannins compose a substantial part of the organic substances that are leached from Alnus then it would appear that this species is predisposed to breakdown. The precise role of the cuticle in restricting losses of substances by leaching is not known, but it is undoubtedly very important. Where the cuticle is thick it is often left intact even after the rest of the leaf has been destroyed. The extreme example of this is Ilex aquifolium, where frequently all that remains of the leaf is an intact bag of cuticle. Such a 'bag' is surprisingly robust and all of the 'whole' Ilex leaves recovered from the Silwood deposit were in this form. The cuticle of the upper leaf surface of Quercus was often similarly left intact on leaves that had been exposed to the lake environment for 8 months.

Microbiological activity clearly affects the mechanical strength of leaves. Whilst it cannot be denied that with most species the loss

of mechanical strength is the result of both macro and microbiological breakdown, the example of Fagus sylvatica illustrates the loss of mechanical strength without any sign of invertebrate attack being evident. Fagus shows little sign of invertebrate attack even after being exposed for eight months in either lake or stream environments (Figs. 28-30), but results of the rolling fragmentation experiment show that loss of mechanical strength, even in this apparently resistant species, is quite considerable (Fig. 47).

Most species appear to exhibit a higher rate of degradation in the stream environment. This is perhaps most clearly shown in the case of Alnus (Figs. 35-37, 40). Examination of the type of destruction, however, suggests that the reason for the greater loss of material in the stream processed leaves, is a combination of both biological and mechanical degradation. The leaves exhibit an angular fragmentation which is characteristic of mechanical damage, rather than the rounded holes typical of the attack by large particle feeders or the skeletal vein pattern produced by microbial degradation and small particle feeders. The contrast may be clearly seen in the case of Quercus (Figs. 31-34). As the leaves become less strong the fluid forces experienced in the stream nylon cages leads to successively greater fragmentation.

As with biological breakdown, mechanical fragmentation is, to some extent, influenced by leaf structure and form. Salix cinerea, for instance, has a strong midrib, and frequently the lamina breaks up, but the pieces remain attached by means of the midrib. Fagus, however, seems to be destroyed by random attrition, while in Quercus the lobes tend to break off, followed by fragmentation of the remaining lamina. As in Salix the midrib tends to hold the pieces together. Alnus, by comparison with the clean breaks of Fagus, tends to tear and,

although much less brittle than Fagus, is easily destroyed once the tissues are weakened by microbial attack.

In most species the mechanical breakdown will take the form of gradual attrition at the margins. If the energy of the environment is sufficiently high, however, then brittle species such as Fagus sylvatica (particularly the 'sun' leaves) may be broken across the midrib. This rarely happens with more pliable leaves. The result of attrition is that where previously the areas of the whole leaves followed a normal distribution, now a bimodal distribution is produced; one peak being composed mainly of the fragmented pieces and the other of the larger remains. This pattern can be seen in both Fagus and Quercus, illustrated in Figs. 44-46, in spite of the slightly different forms of their fragmentation. The complex nature of the curves limits the use of such statistics as the median and mode, thus the measures of fragmentation presented in Figs. 47-50 are based on average fragment area. It should be pointed out, however, that these estimates are probably higher than is actually the case since, for practical purposes, a lower limit had to be put on the size of fragments that were going to be counted after rolling. This lower limit was chosen to be 25 mm^2. By observation, however, the number of fragments falling below this size, for the conditions of the experiment, was found to be low. Apparently the forces experienced by a piece of leaf smaller than 50 mm^2 were insufficient to break it, but further microbiological attack would probably lead to greater fragmentation.

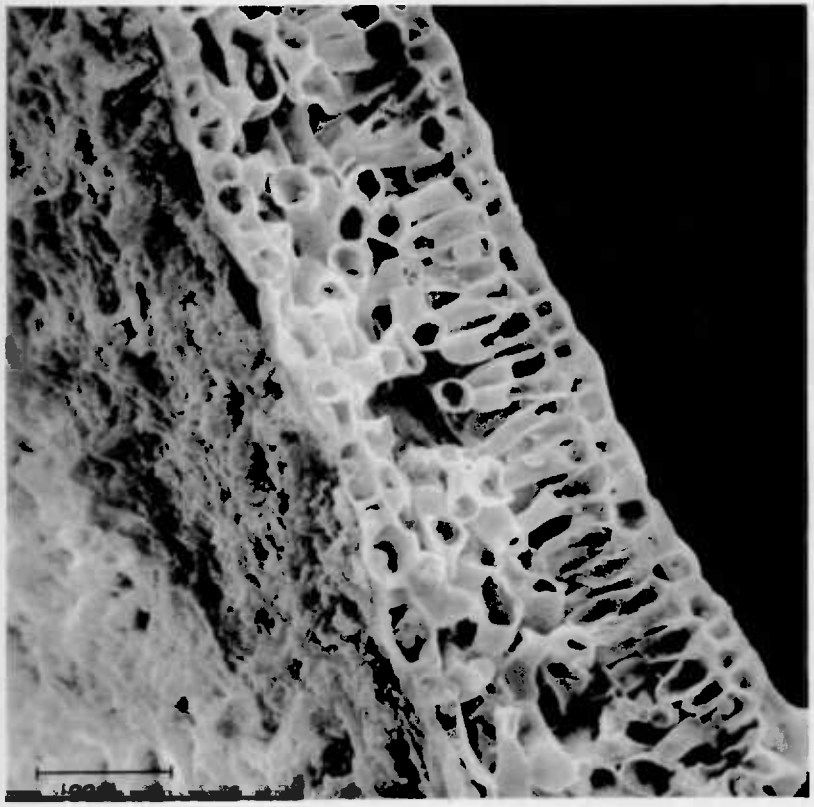
Chaney and Sanborn (1933) considered that a thin leaf has only half the chance of entering the fossil record as a thick one, all other things being equal. To test this opinion Ferguson (1971) cut discs of fresh leaves from eleven species (which covered a range of different leaf thicknesses) and rotated them with sand and water in a revolving drum.

Each run lasted 100 hours and was repeated three times, but even after this treatment all species showed little sign of wear. It therefore seems unlikely that leaf thickness contributes much to the potential probability that a leaf will be preserved in the fossil record. The results of experiments with whole fresh leaves also show little breakdown compared with leaves exposed to microbiological attack. Thus, unless the leaf is excessively large (or small), leaf size, as well as thickness, is unlikely to be as important a factor in determining the preservation potential of a leaf type as the rate of microbiological degradation.

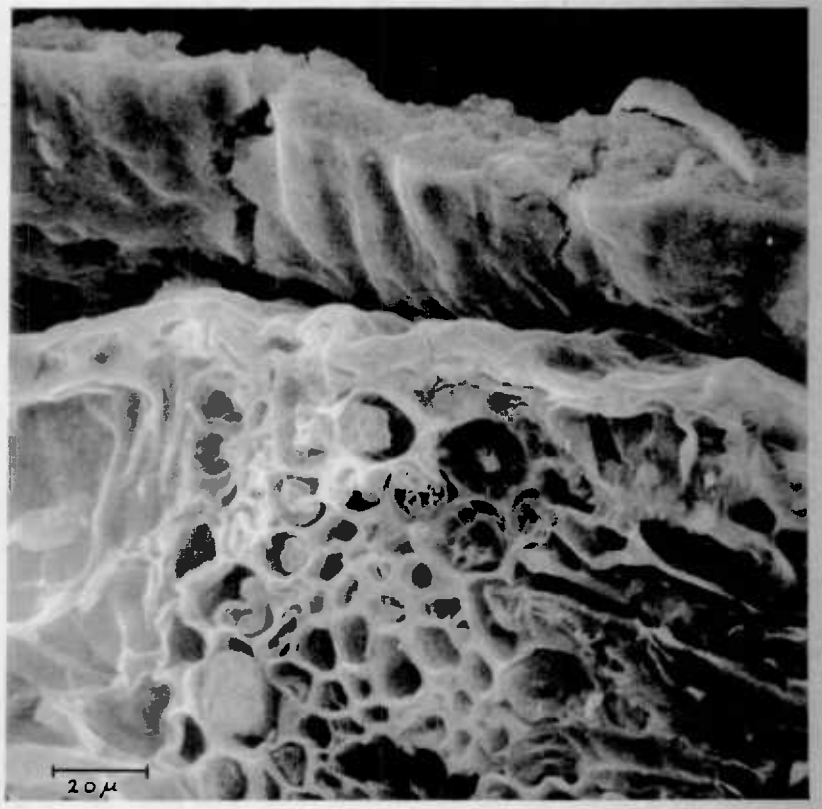
Cuticle thickness is often proposed as an important factor as regards the preservation of a leaf. It is certainly true that the cuticle is far more resistant to breakdown than, for example, cellulose or lignin (White, 1933), however the cuticle is not necessarily such an effective barrier to the microbiological colonization of the leaf tissues as is sometimes supposed. The example of Ilex aquifolium, when frequently all that remains is an intact 'bag' of cuticle, has already been mentioned. De Vries et. al. (1967) have reported that, in the process of cuticle degradation, attack begins on the surface originally in contact with epidermal cells, and the cutin of the anticlinal walls is the first to be affected. Thus destruction of the leaf material may well take place from the inside and not externally. More extensive cuticle degradation may be prevented by the external coatings of extremely resistant (White, 1933) waxes.

It was noted that many leaves present in the Silwood stream become coated with a layer of sediment within one or two weeks from entering that environment. This encrustation may also limit external microbiological attack. Plate 4(a) shows the nature of this encrustation on the external surfaces of a Fagus sylvatica leaf extracted from

PLATE 4.



a) An S.E.M. photograph of a freeze dried transverse freeze fracture of a Fagus sylvatica leaf recovered from the delta. The lower surface of the leaf can be seen to be covered with an encrustation of sediment.



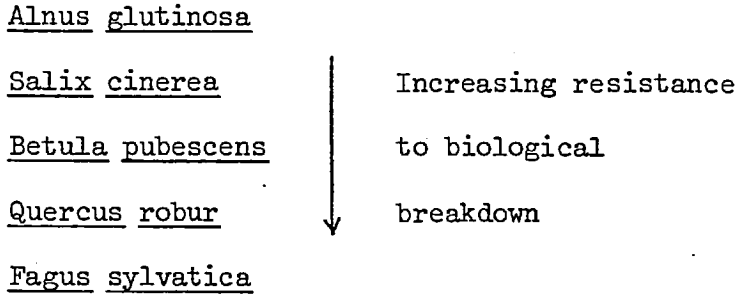
b) An air dried leaf of Fagus sylvatica recovered from the stream. Here the surface encrustation has curled back from the leaf during drying to reveal the faithful impression of the leaf surface.

the surface of the delta deposits. The coat is extremely difficult to remove (this cannot be achieved by washing) and is surprisingly coherent even when dry. Plate 4(b) also demonstrates the faithful replication of the leaf surfaces formed by this crust. X-ray microanalysis of the encrustation in contact with the leaf surface shows that it is almost entirely composed of ferric hydroxide/oxide flocs, whereas the surface of the crust exposed to the stream water contains significant concentrations of silicon (Fig. 99). Thus the epidermal features of the leaf become preserved in the fine grained iron flocs in spite of the coarser nature of some of the bulk sediment components such as quartz grains and diatom frustules. The mechanism for the original deposition of the iron on the surface of the leaf is not understood, but it may well be of biogenic origin. The coherent nature and rapid formation of this encrustation may account for the high quality impression fossils that are found even in a coarse grained matrix (e.g. The Dakota Sandstone fossils from Kansas).

Because most fragmentation occurs after some microbiological breakdown of the tissues has taken place, fragmentation during the floating period will be minimal. Consequently, it is not until the leaf becomes saturated, and is transported in suspension or as part of the bedload, that the main process of fragmentation begins. Thus floating times of as little as two or three days may mean that it is possible for some leaves to be transported great distances before they begin to be fragmented. These species may, therefore, depending on the size of the source area, be frequent, or even common, in their eventual depositional environment.

The upper limit to the distance a leaf may be transported in suspension, or as part of the bedload, and still be recognisable, is determined by the fragmentability of the leaf. The five species

investigated from the Silwood environment may be placed in an increasing order of resistance to biological breakdown as follows:



The differential destruction of leaves during water transport depends on an interplay between potentially destructive environmental conditions and the characteristics of the leaves of the various species controlling the degree of degradation.

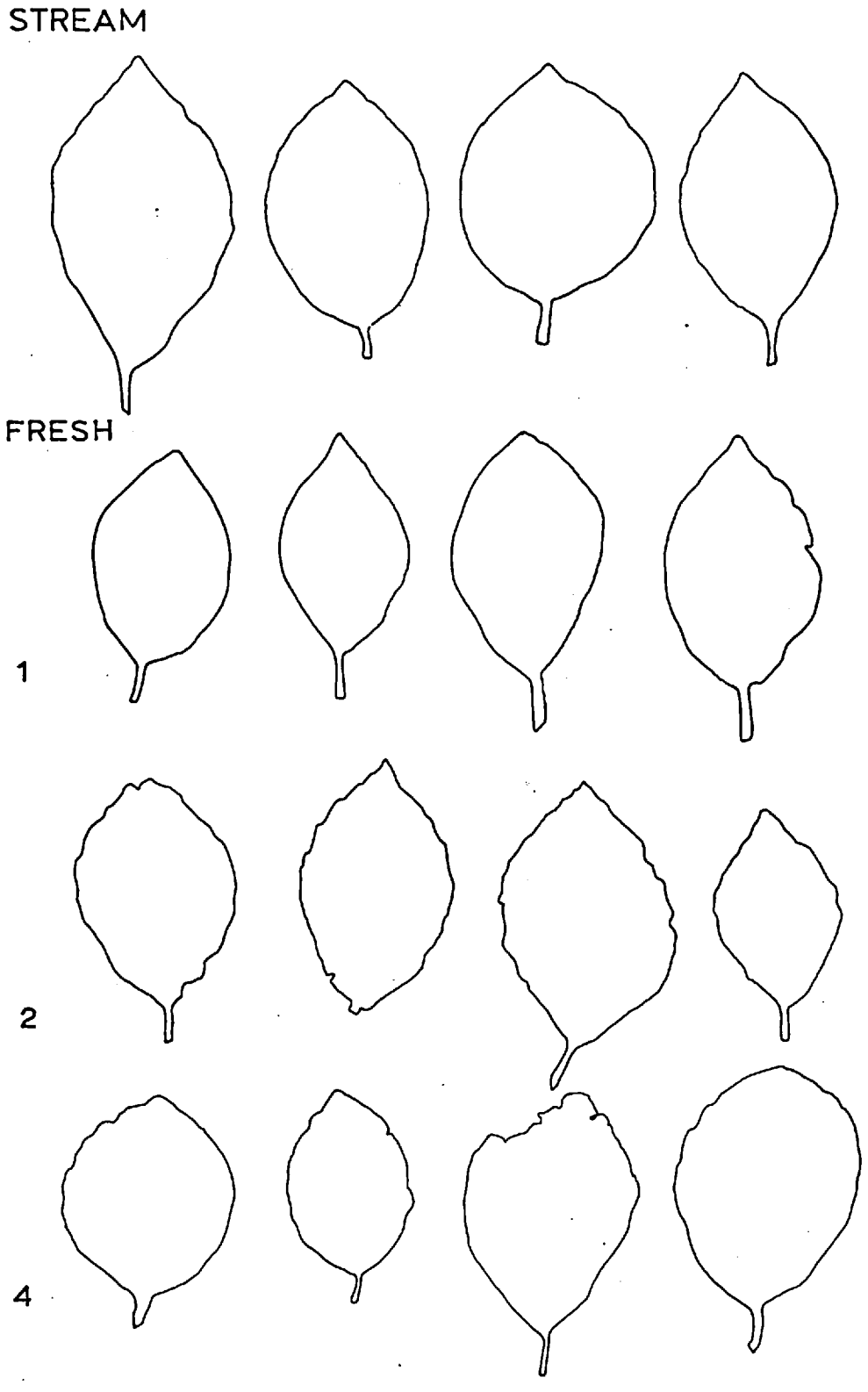


Fig. 28. Fagus sylvatica leaves showing little degradation after 1, 2 and 4 months exposure to the stream environment.

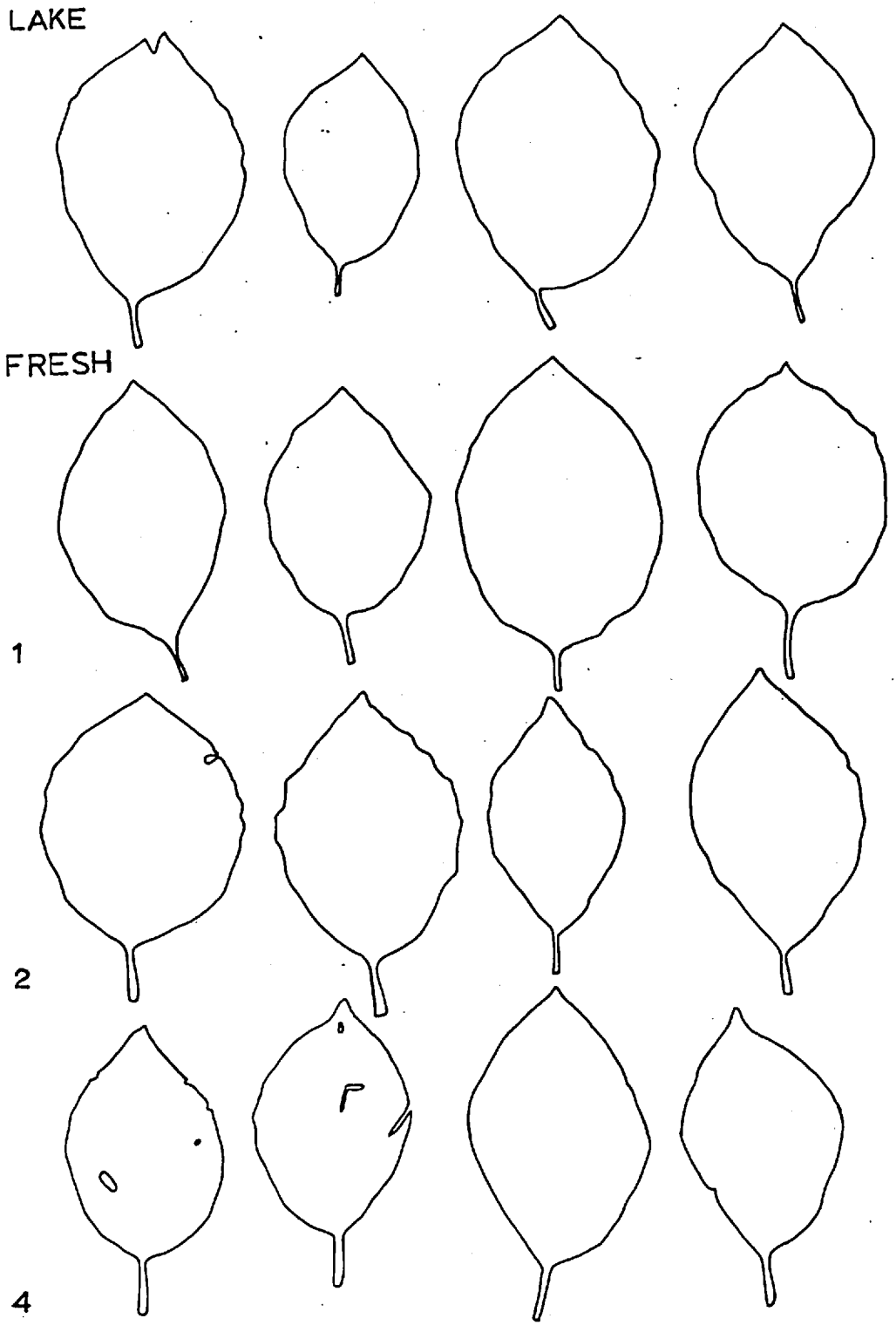


Fig. 29. Fagus sylvatica leaves freshly fallen and after 1, 2 and 4 months on the lake bottom.

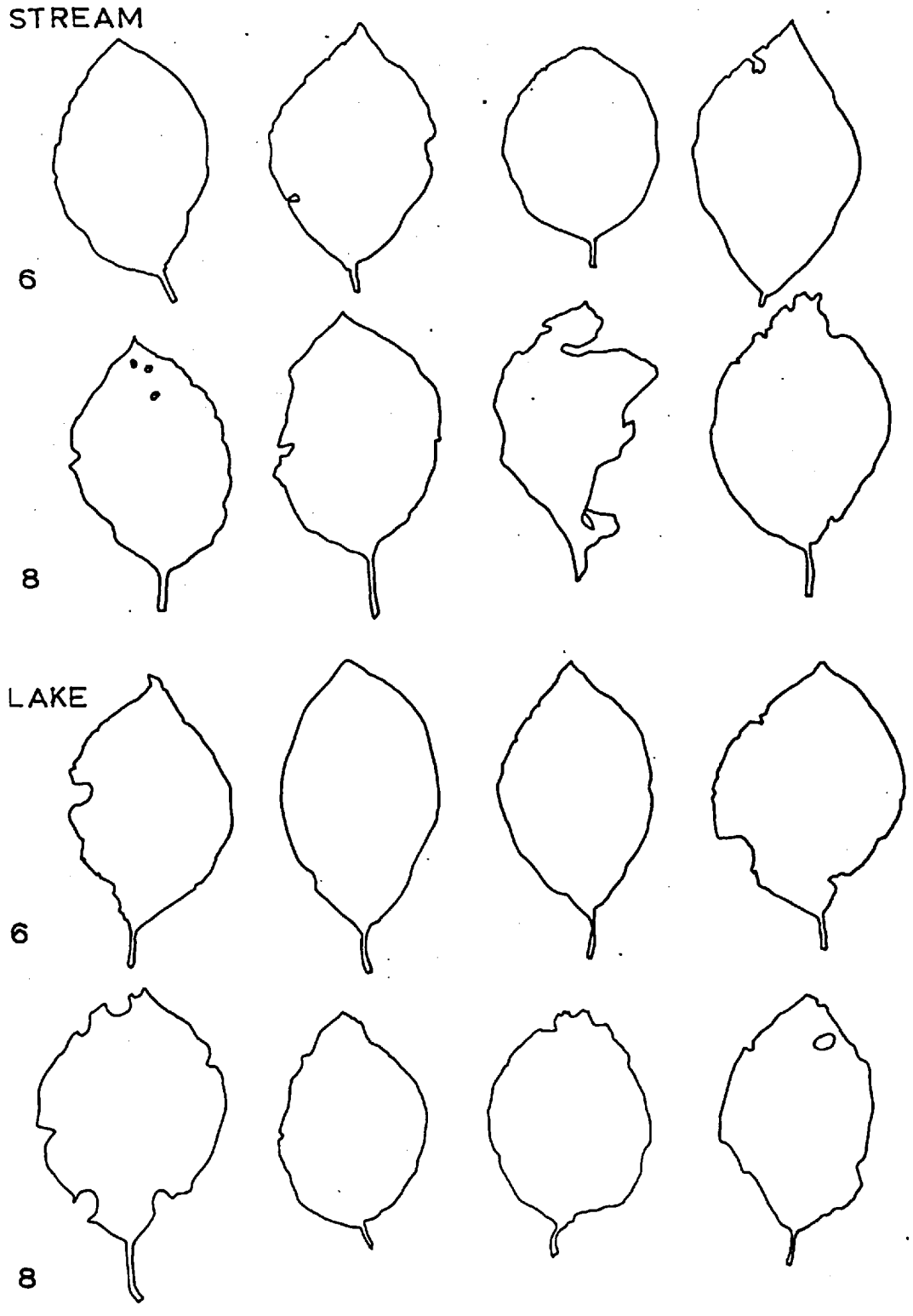


Fig. 30. Fagus sylvatica after periods of 6 and 8 months in both stream and lake environments.

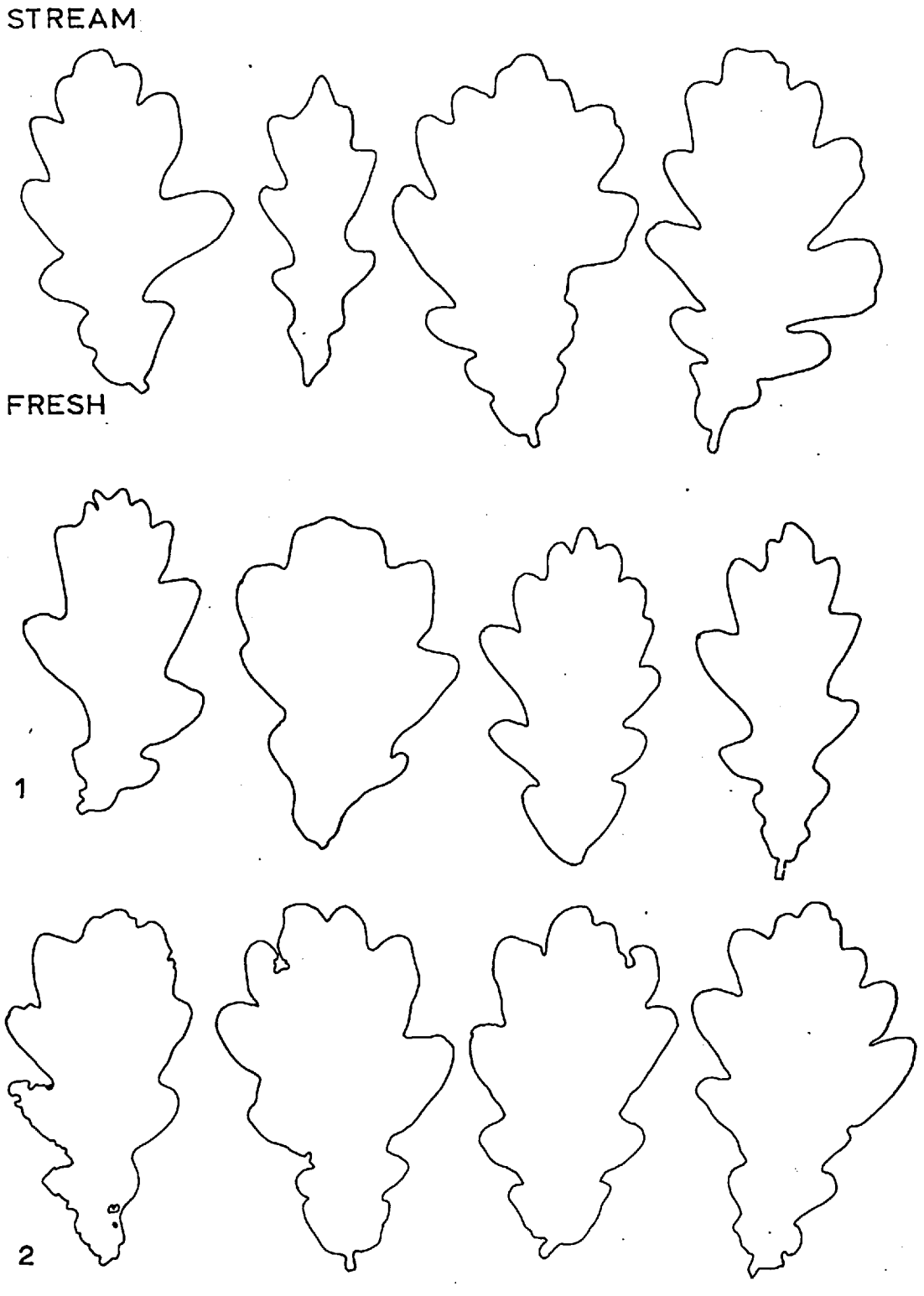


Fig. 31. Quercus robur fresh and after exposure to the stream for 1 and 2 months.

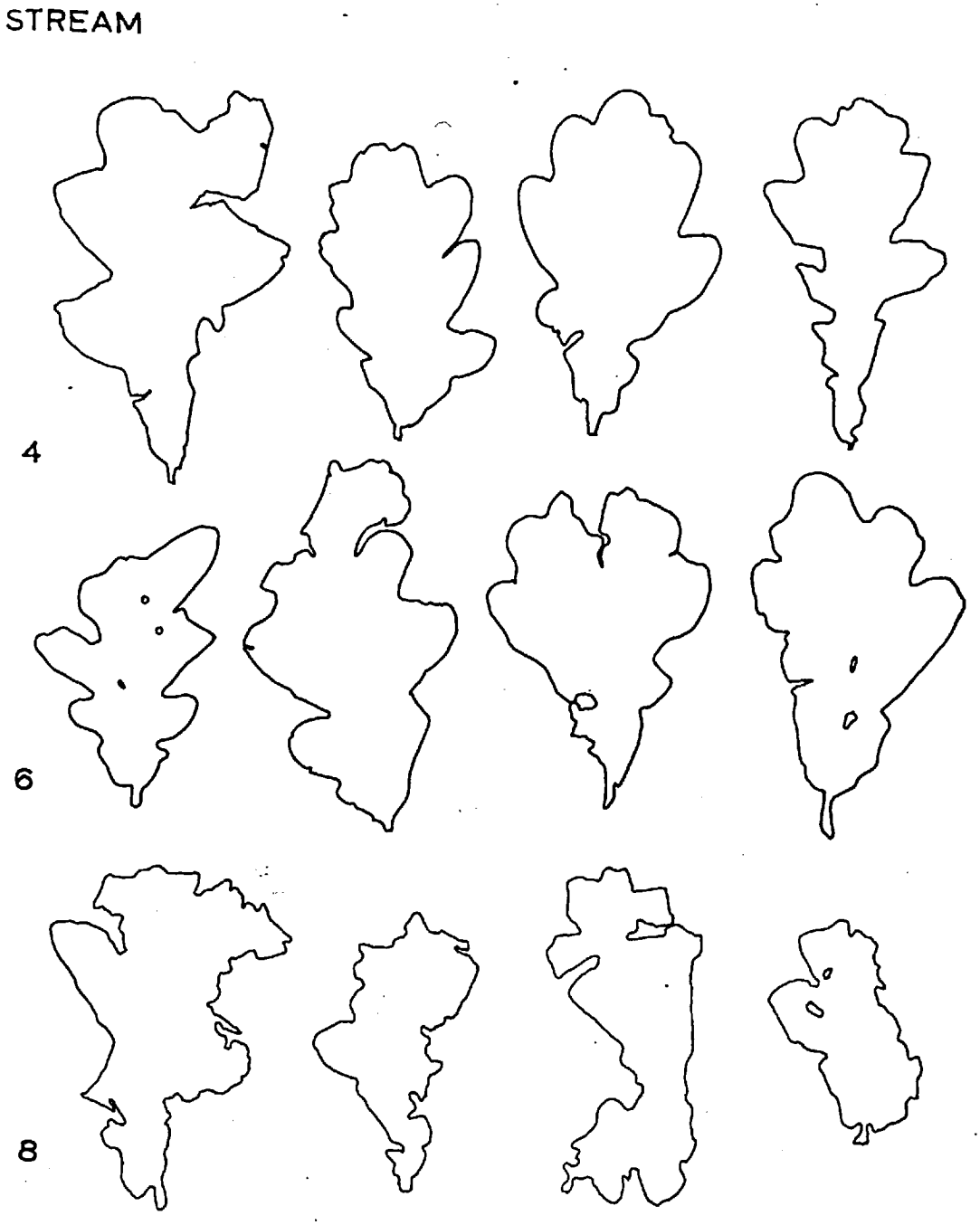


Fig. 32. Quercus robur after 4, 6 and 8 months exposure to the stream conditions.

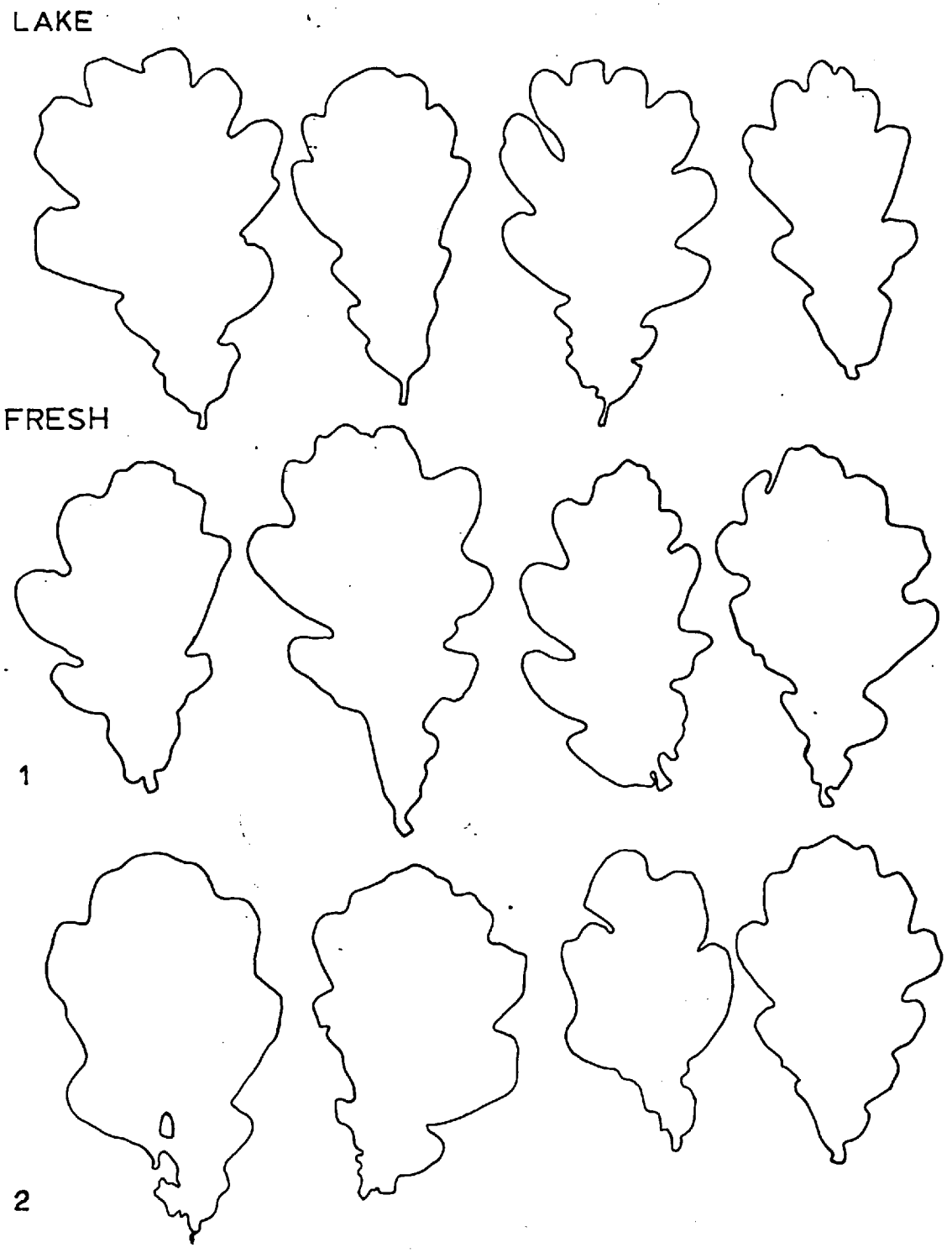


Fig. 33. Quercus robur showing little sign of degradation after 1 and 2 months on the lake bottom.

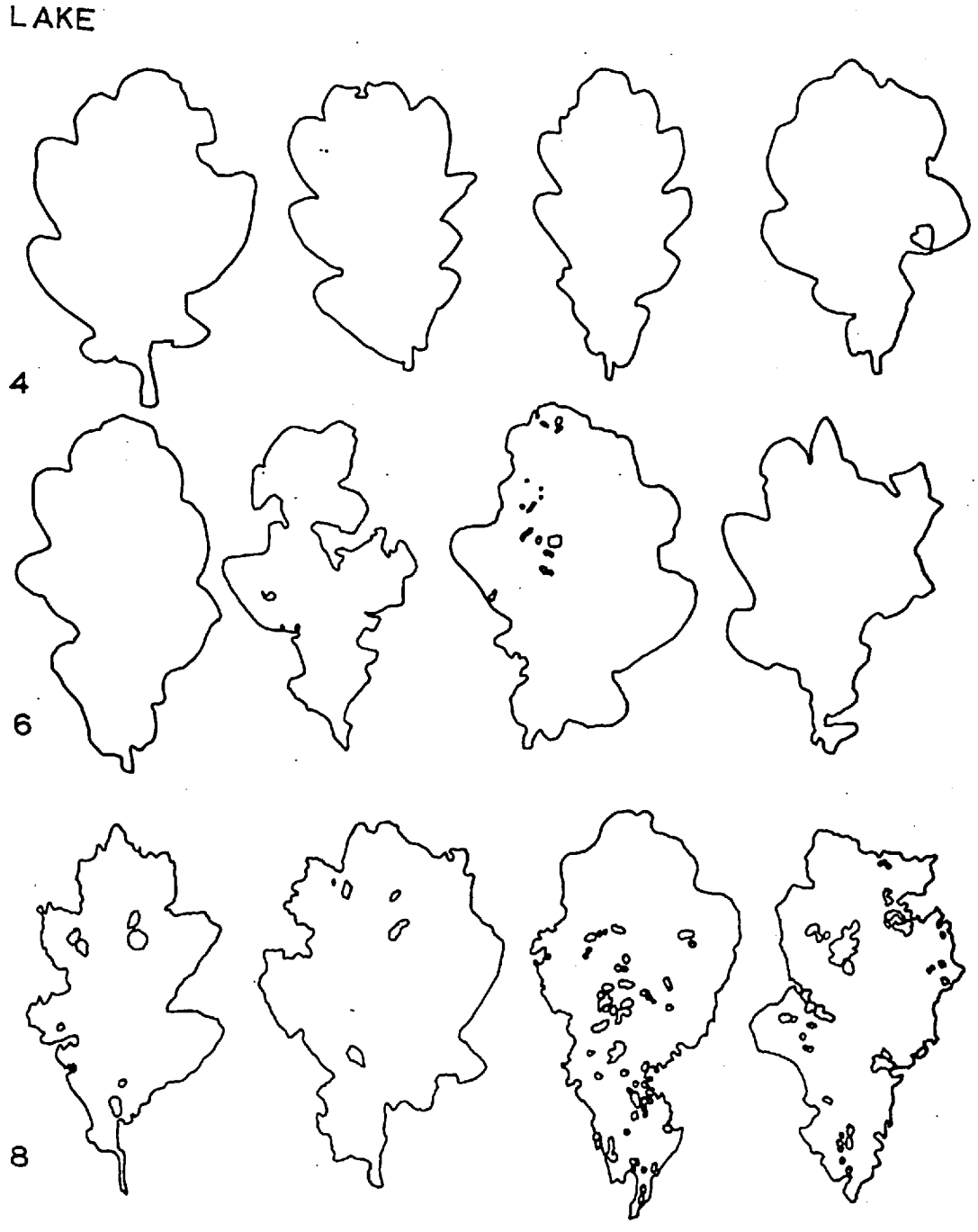


Fig. 34. Quercus robur after 4, 6 and 8 months in the lake.

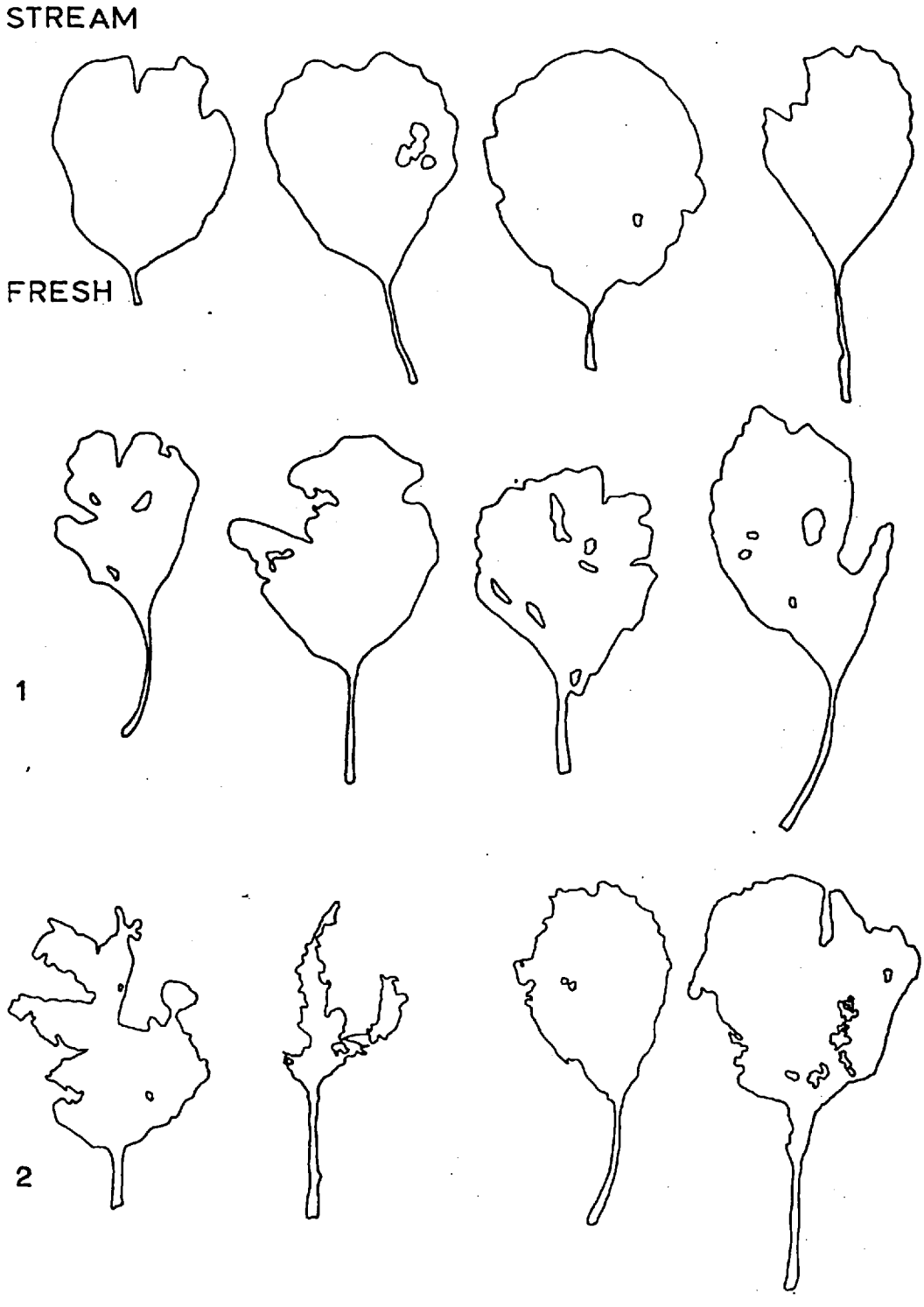


Fig. 35. Alnus glutinosa leaves freshly fallen and after 1 and 2 months exposure to the stream environment.

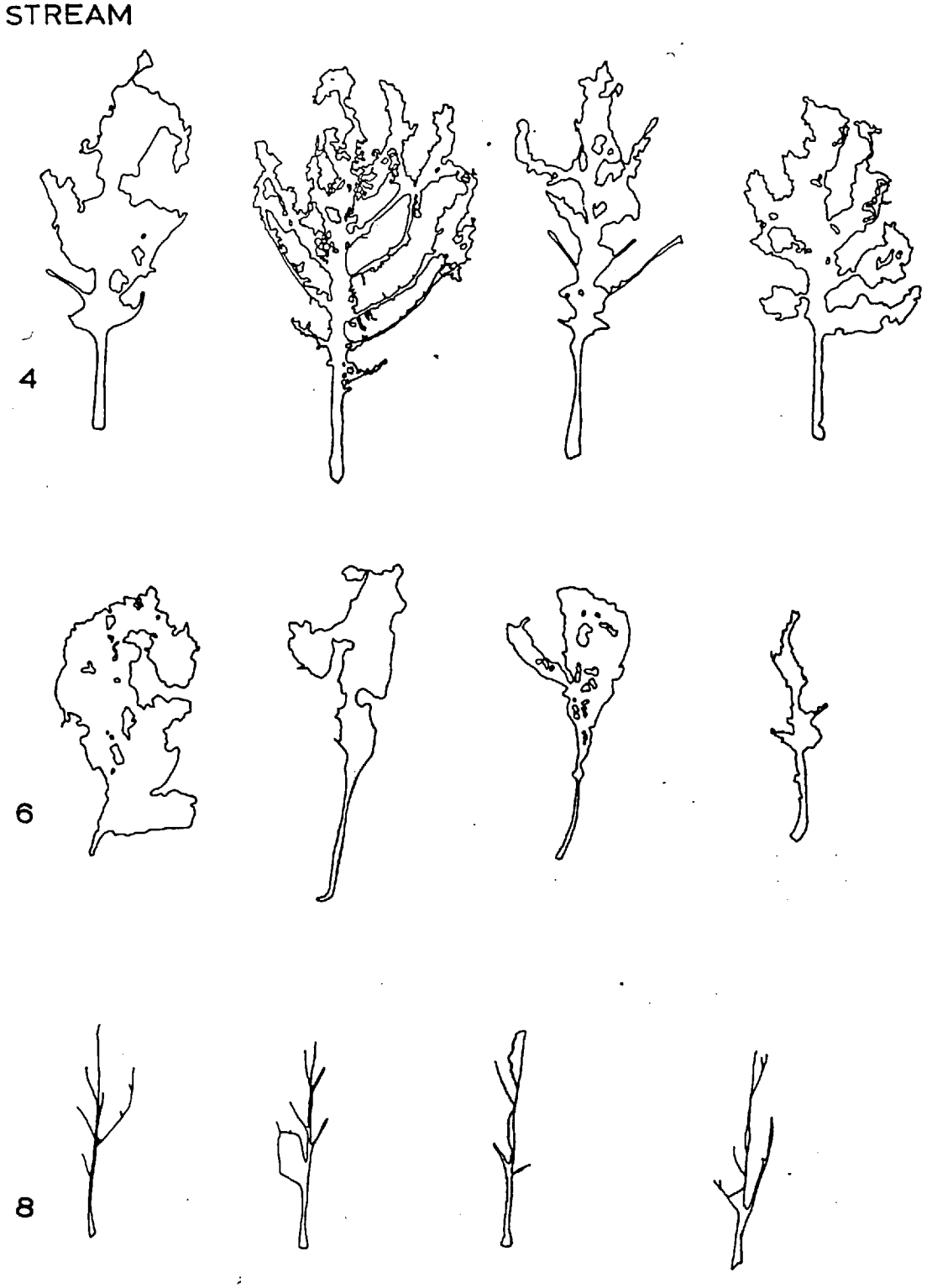


Fig. 36. The degradation of Alnus glutinosa Gaertn. leaves after 4, 6 and 8 months exposure to the stream environment.

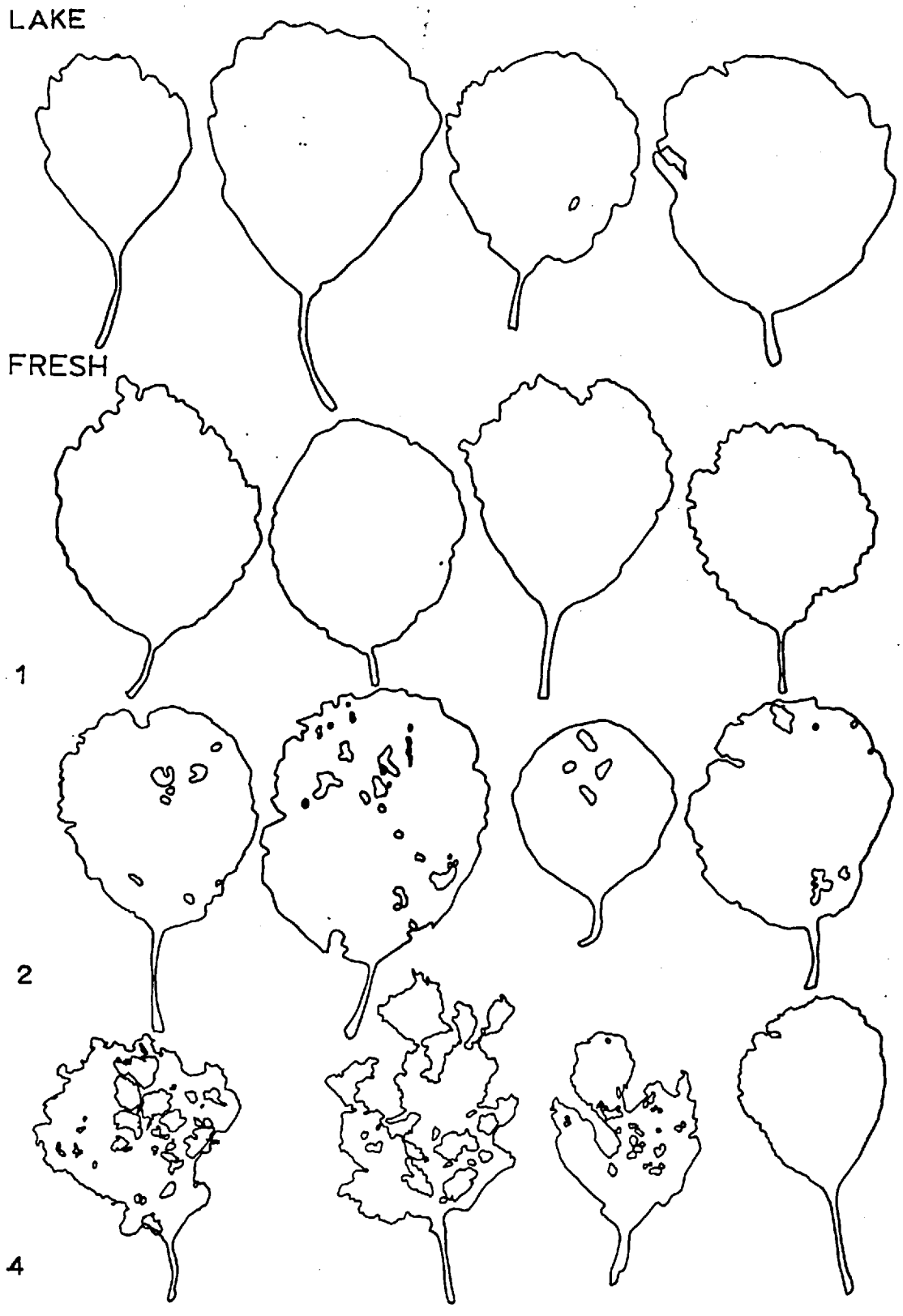


Fig. 37. Alnus glutinosa freshly fallen leaves and examples of the degradation experienced during 1, 2 and 4 months exposure to the lake bottom environment.

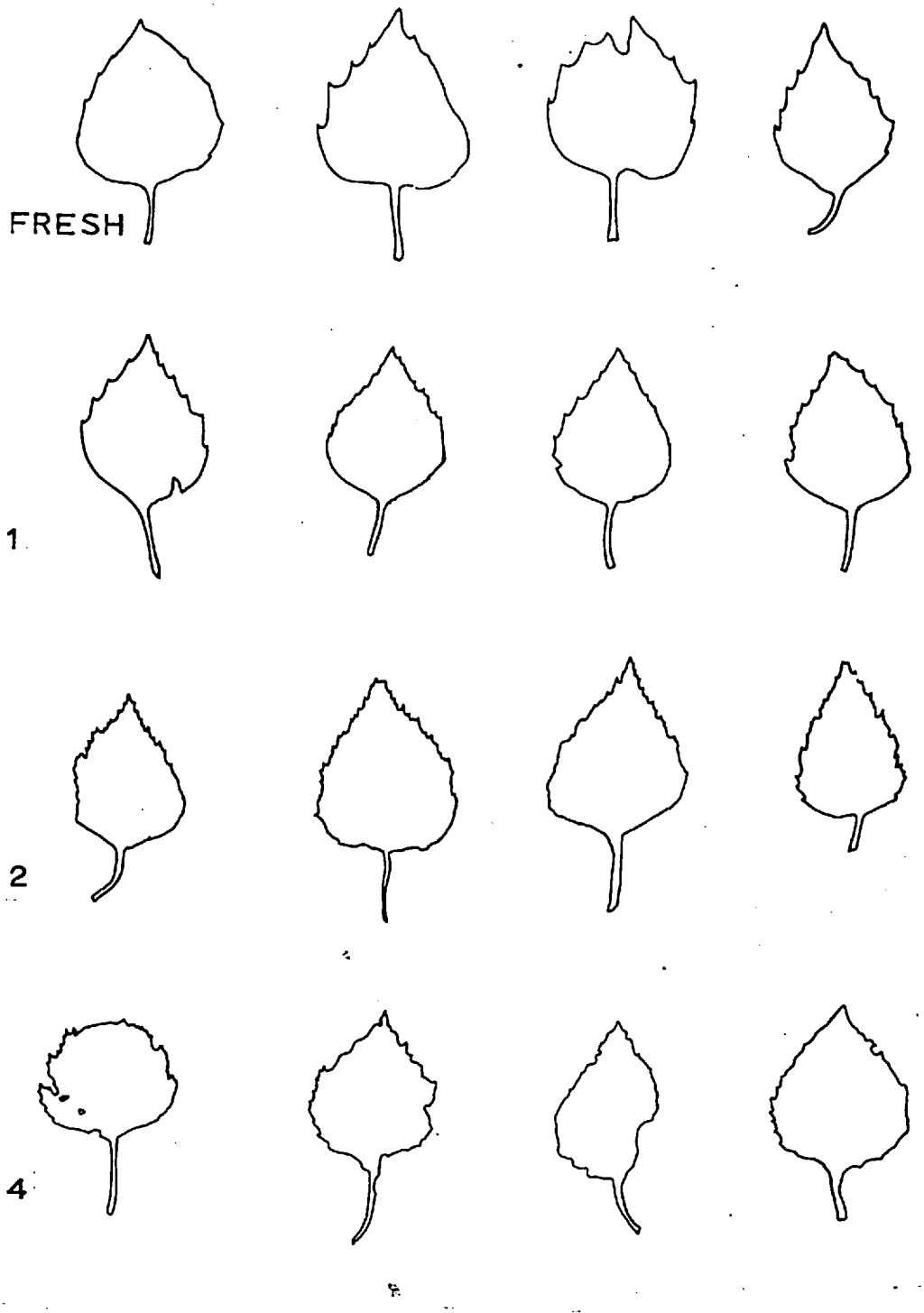


Fig. 38. Betula pubescens leaves freshly fallen and after 1, 2 and 4 months exposure to the stream environment.

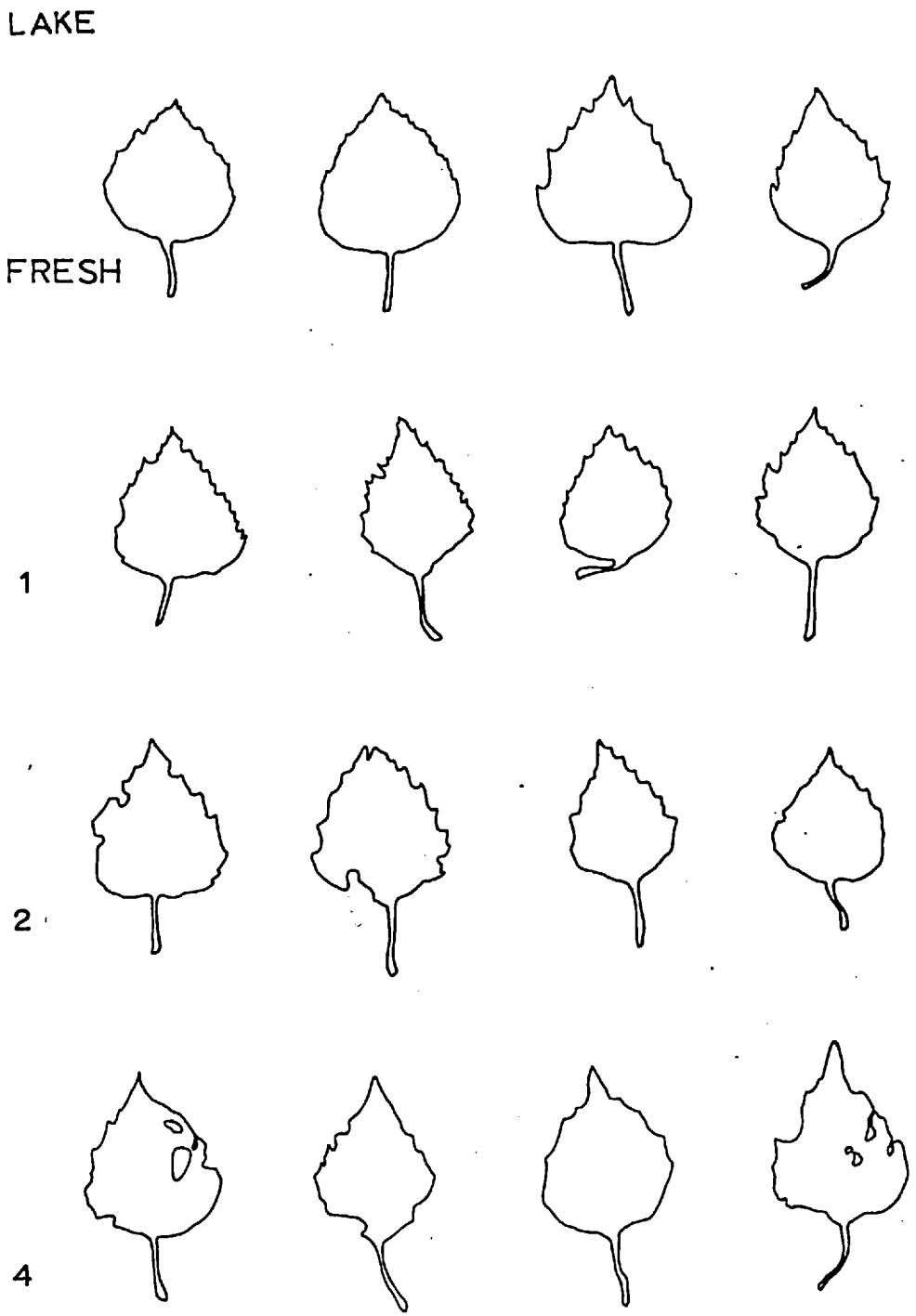


Fig. 39. Betula pubescens showing little sign of degradation even after 4 months on the lake bottom.

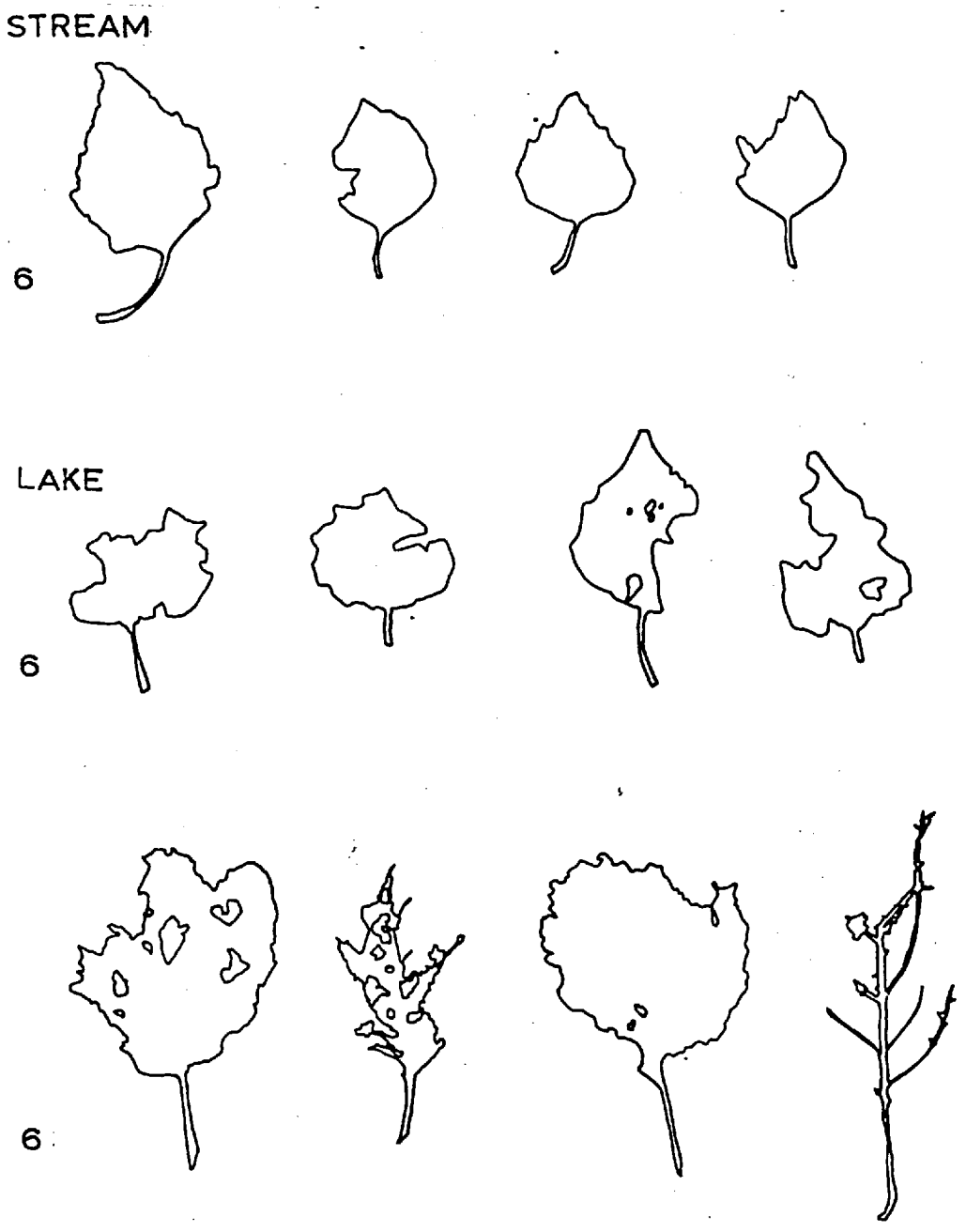


Fig. 40. Top - Betula pubescens leaves after 6 months in the stream. After 8 months only fragments remained.

Middle - Betula pubescens leaves after 6 months on the lake bottom. Again, after 8 months only fragments remained.

Bottom - Alnus glutinosa after 6 months in the lake. After 8 months only fragments and midribs remained.

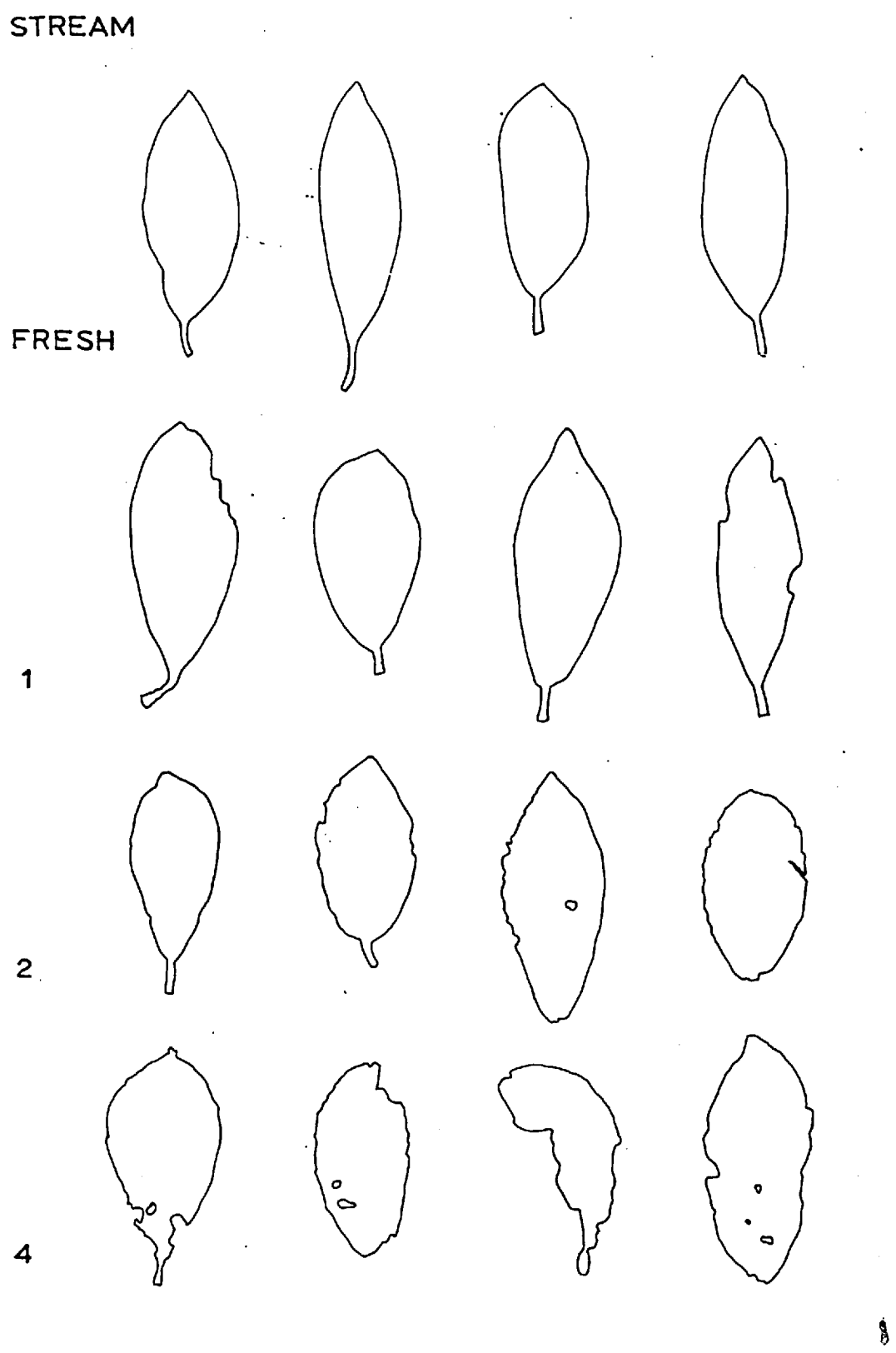


Fig. 41. Salix cinerea fresh, and after 1, 2 and 4 months exposure to the stream environment.

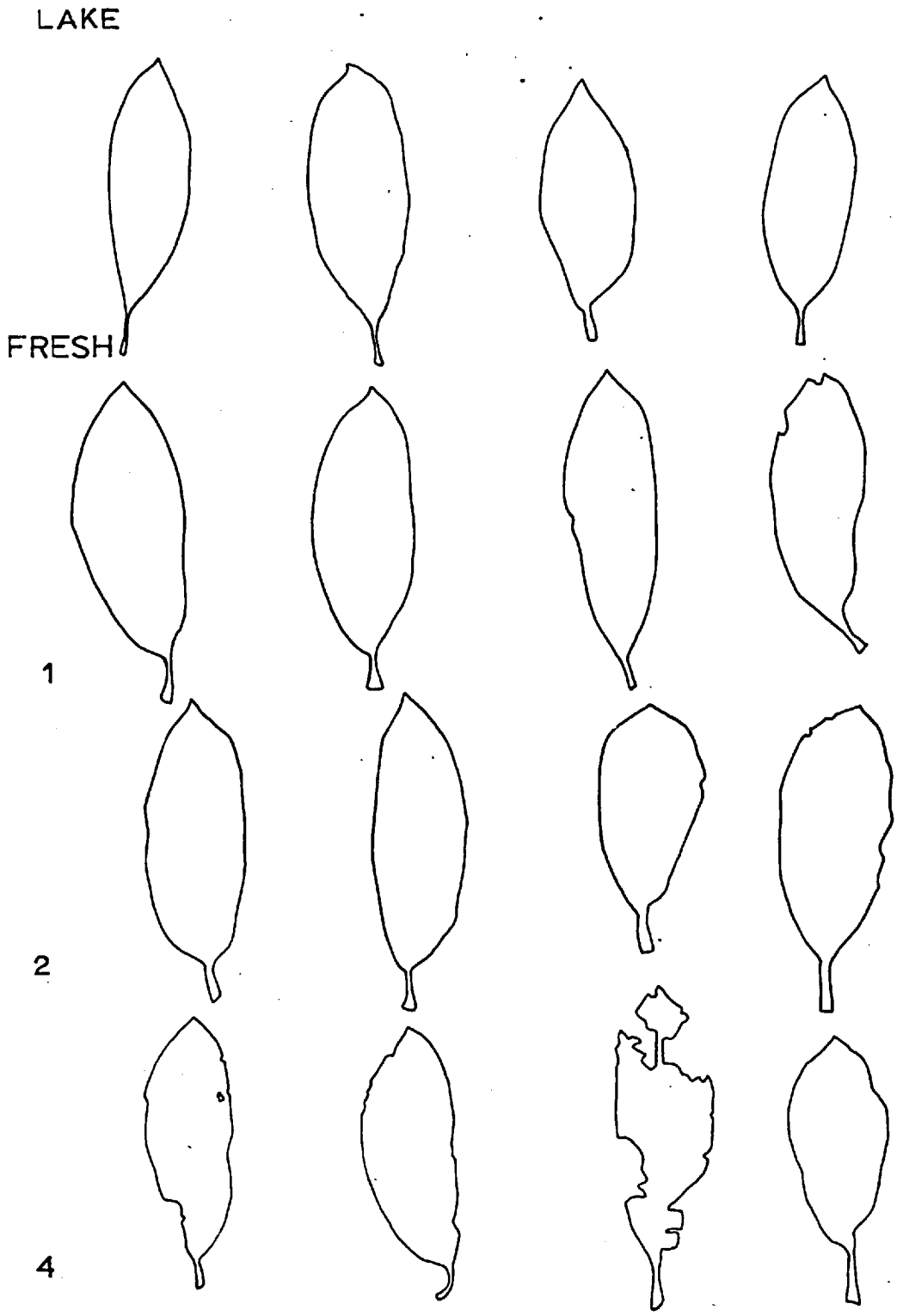


Fig. 42. Salix cinerea fresh, and after 1, 2 and 4 months exposure to the lake bottom environment.

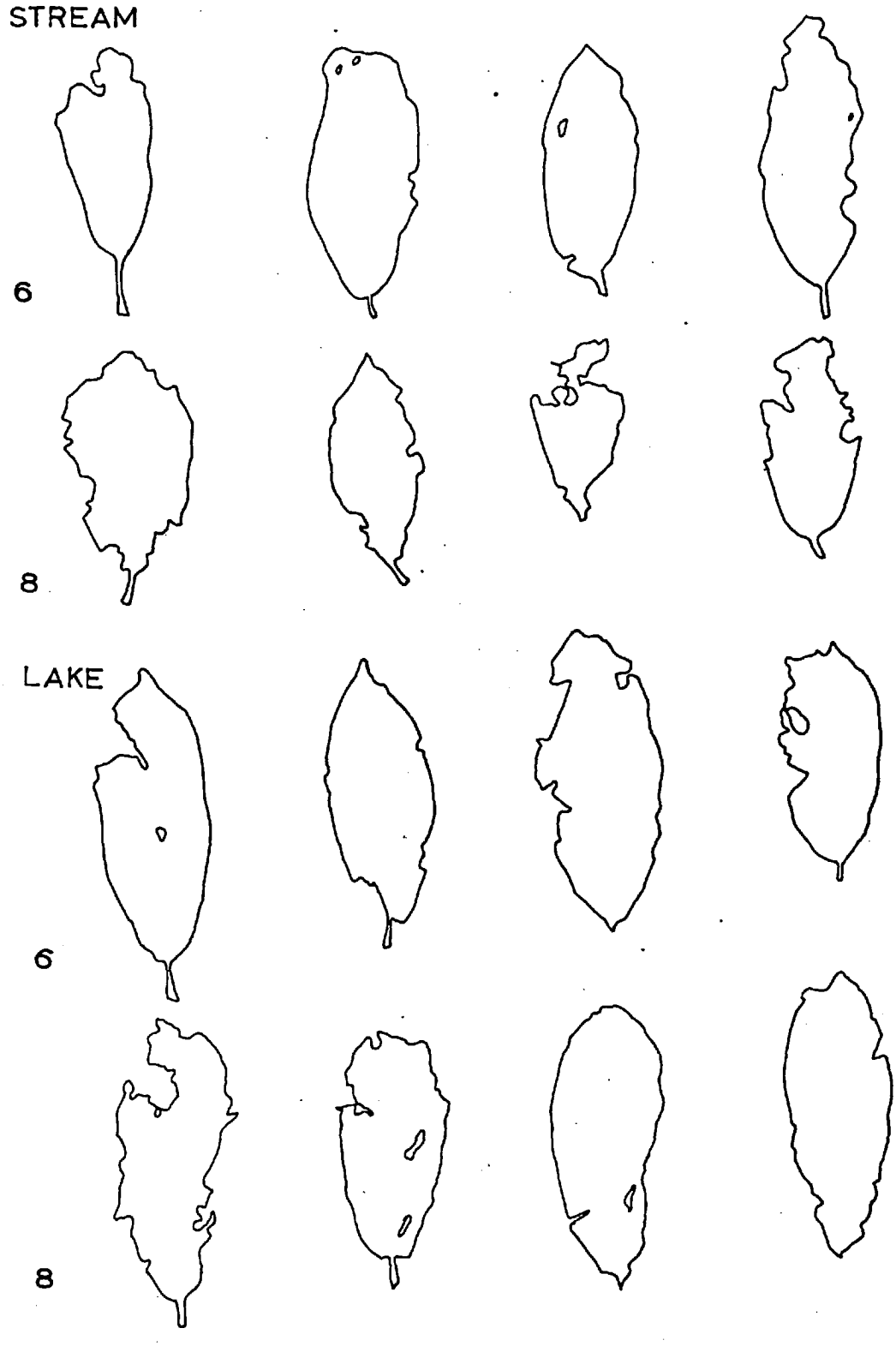


Fig. 43. Salix cinerea leaves after 6 and 8 months in both stream (above) and lake (bottom) environments.

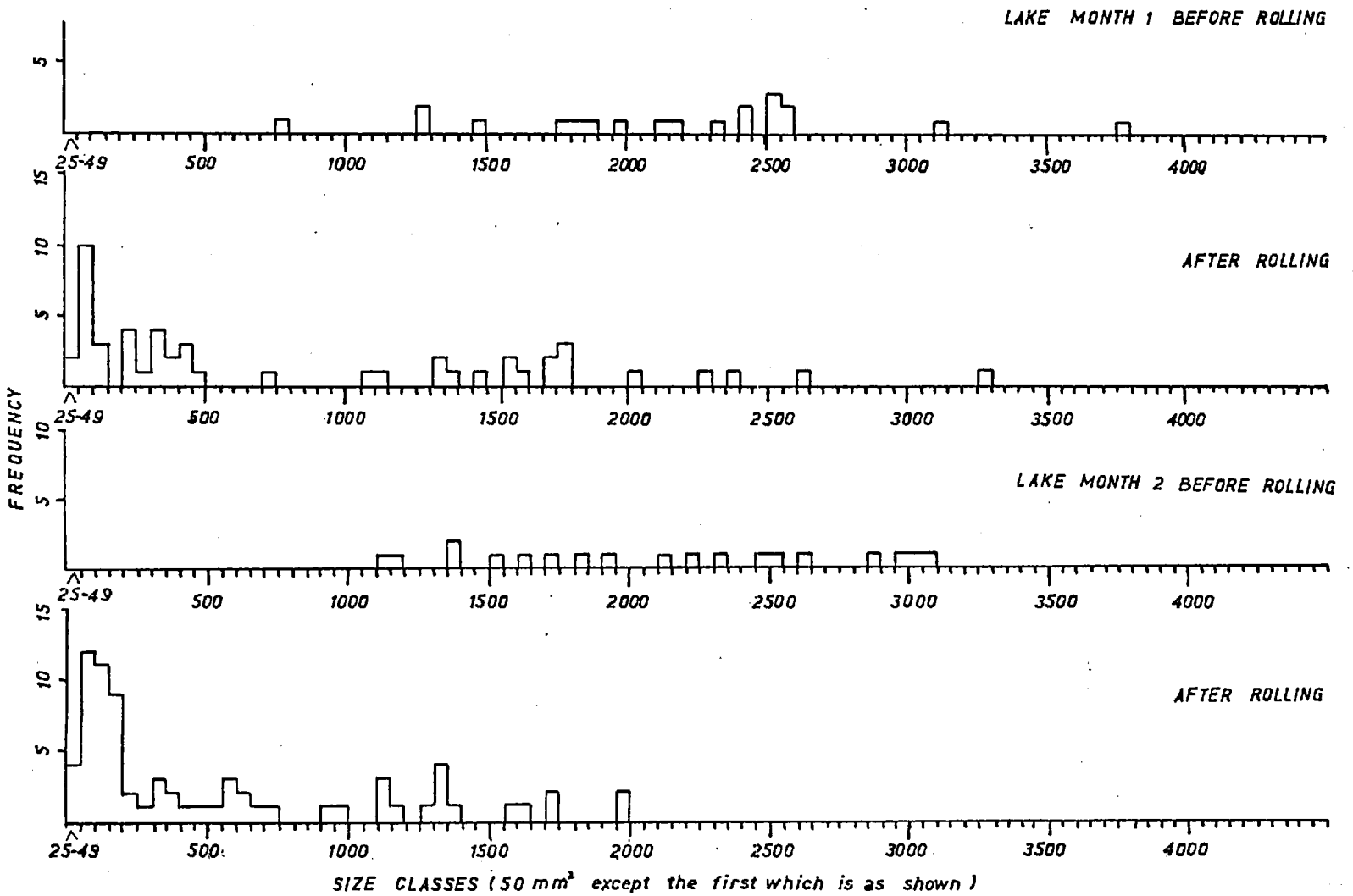


Fig. 44. Size distributions of both whole leaves and fragments of Fagus sylvatica before and after rolling.

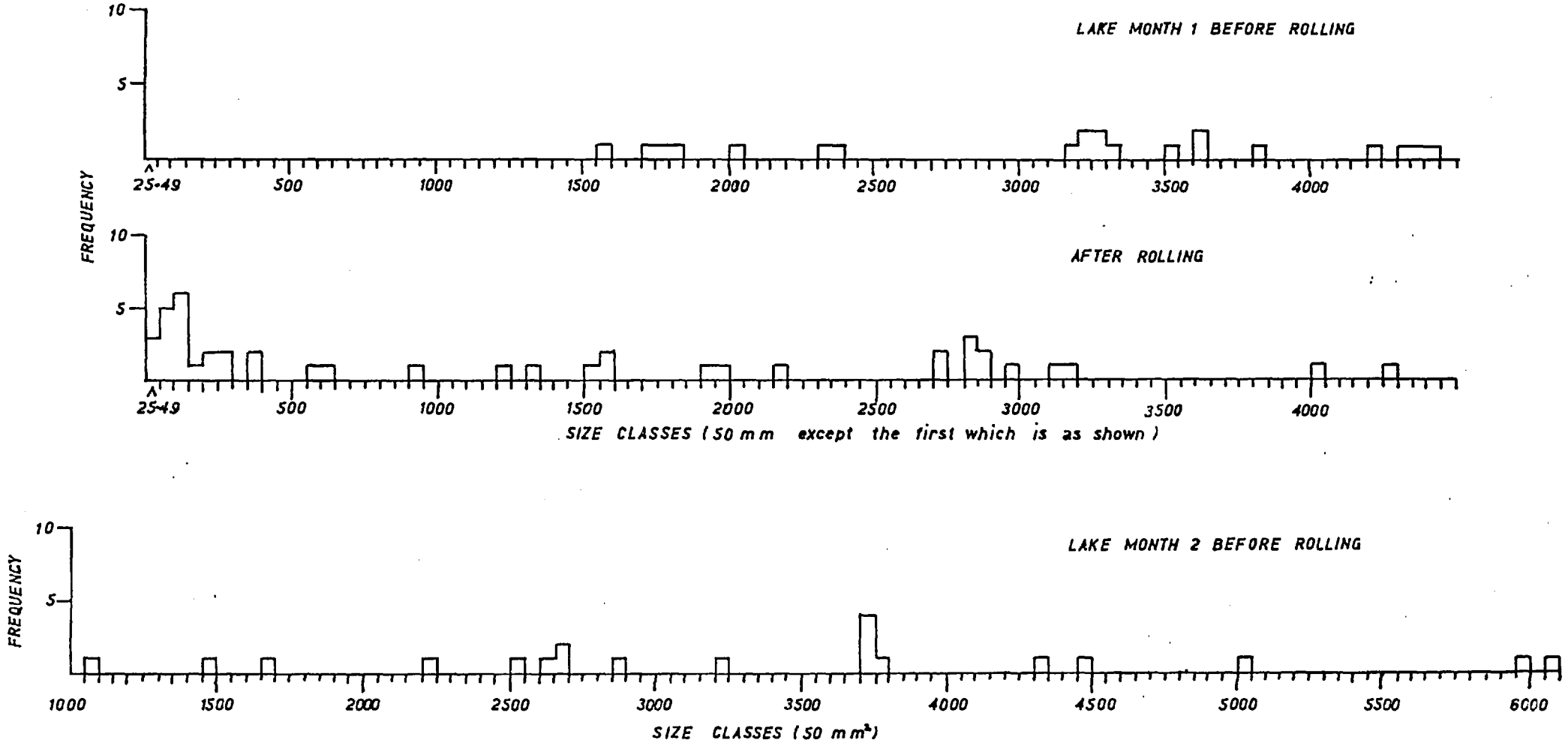


Fig. 45. Size distributions of Quercus robur whole leaves and fragments both before and after rolling.

Fig. 46. Size distribution of Quercus robur fragments produced by rolling leaves that had been on the lake bottom for 2 months.

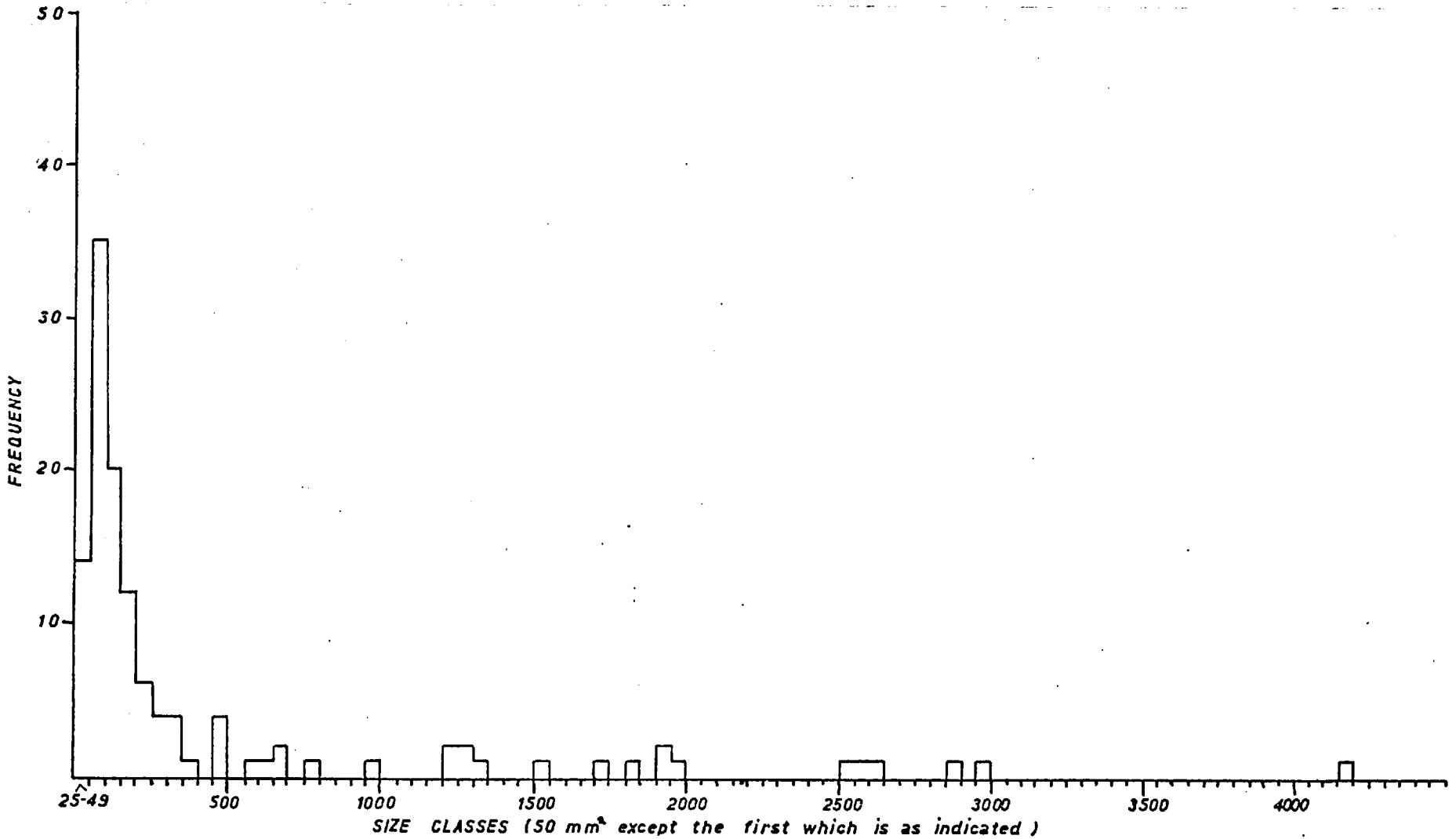


Fig. 47. Results of the rolling degradation experiment with Fagus sylvatica after various periods of exposure to lake and stream environments.

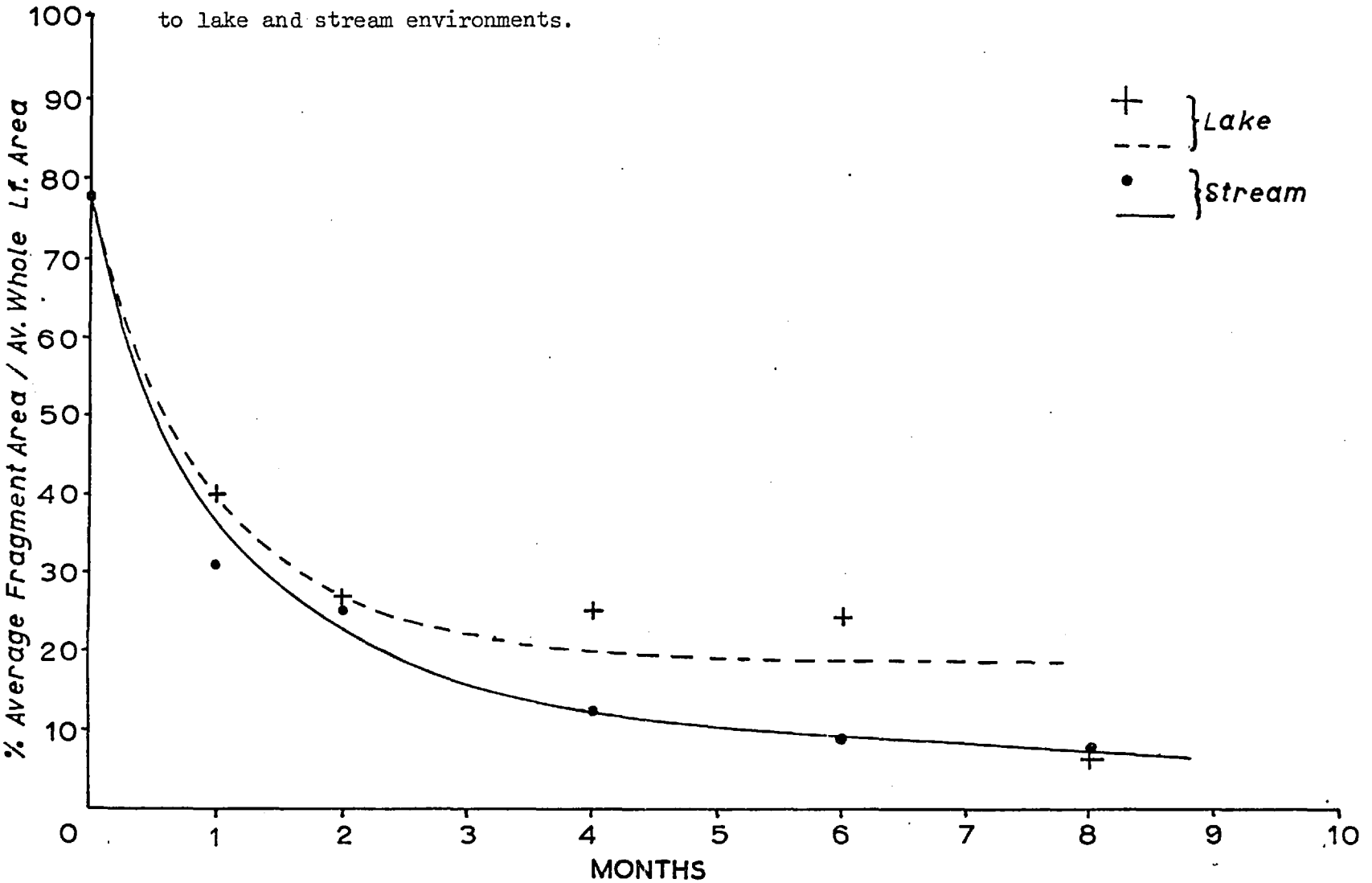


Fig. 48. Results of the Quercus robur rolling degradation experiments.

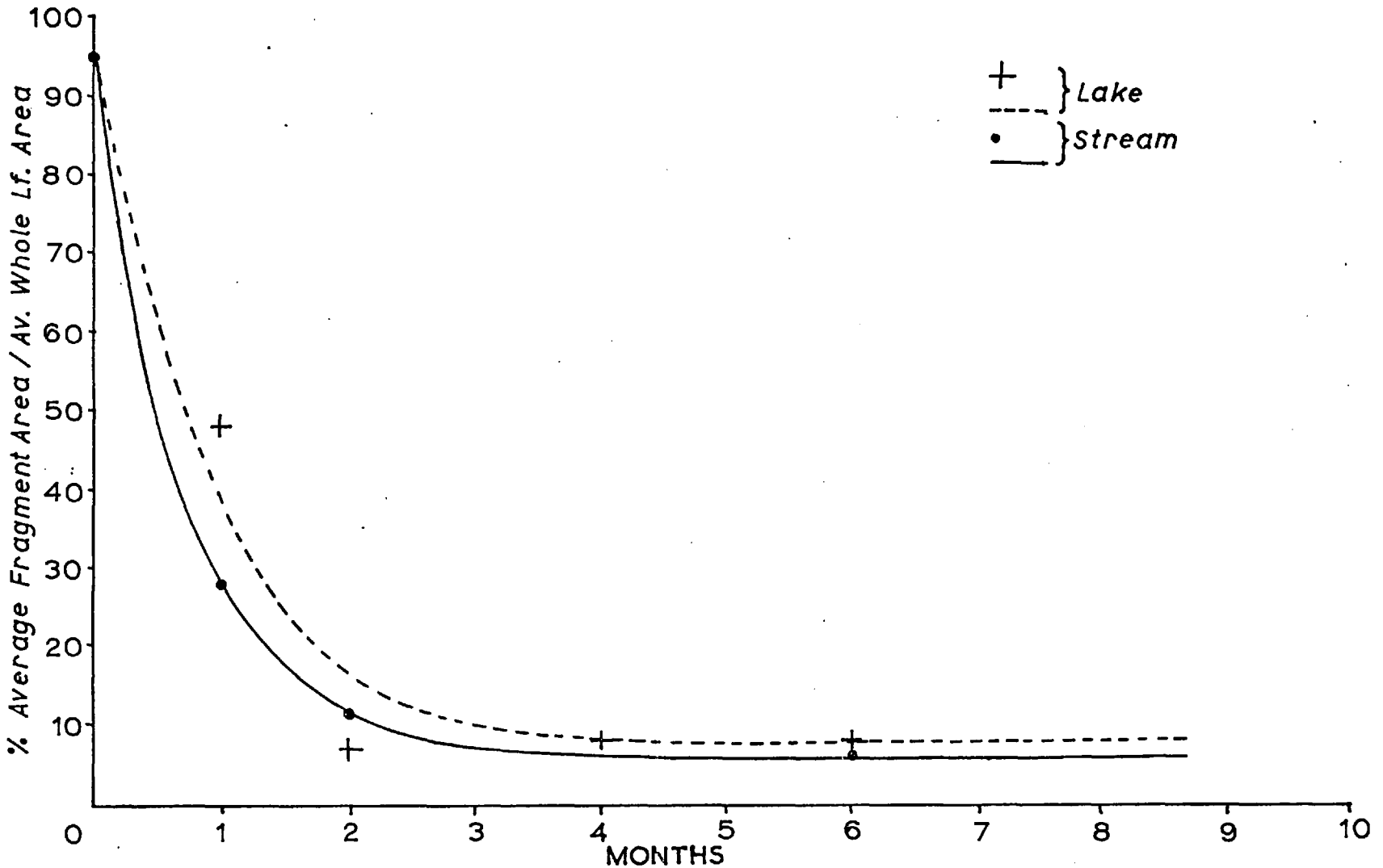


Fig. 49. Results of the Betula pubescens rolling degradation experiment.

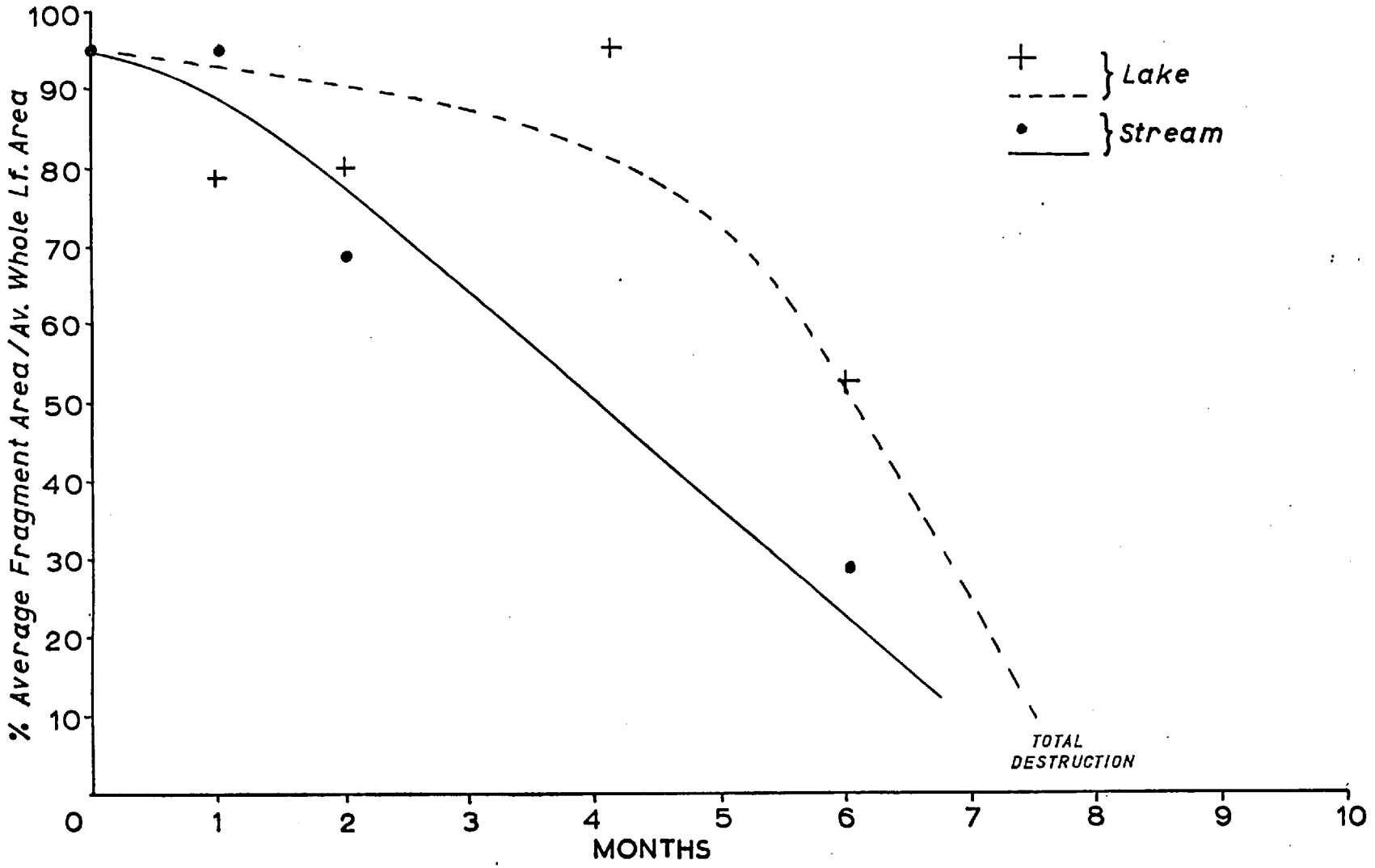
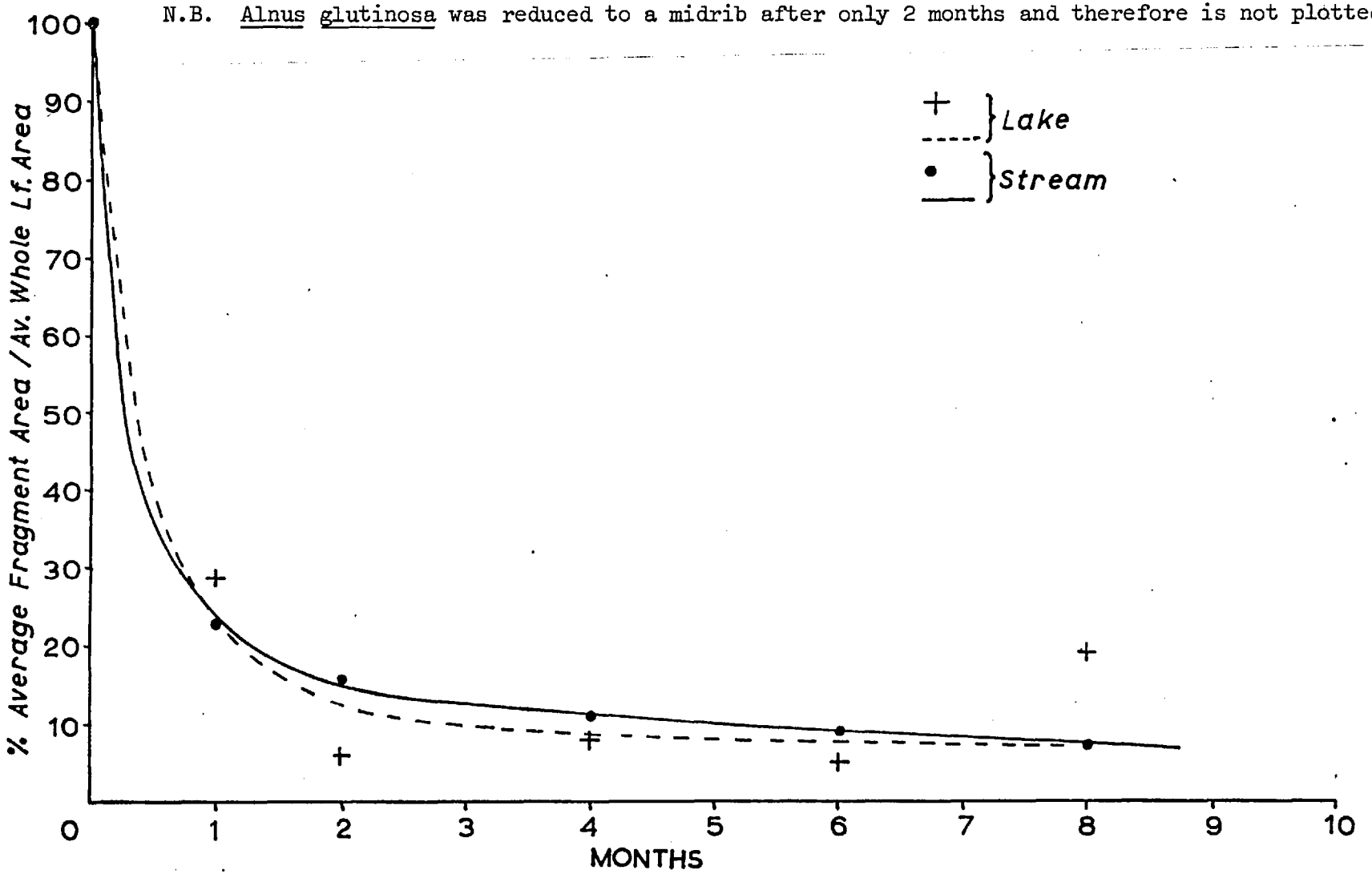


Fig. 50. Results of the Salix cinerea rolling degradation experiment.

N.B. Alnus glutinosa was reduced to a midrib after only 2 months and therefore is not plotted.



FLUID DYNAMICS IN RELATION TO LEAF TRANSPORT

The movement of sediment grains by flowing water has received much attention from sedimentologists. Many hydrodynamic concepts, developed in other branches of science, have been employed by making certain assumptions about the sedimentary particles e.g. that the grains approximate to spheres and do not interfere with each other. Clearly, it would be desirable to determine the hydrodynamic properties of leaf material in order to isolate those characteristics that may lead to sorting during transport.

P. Mantz (1973) has shown that for solid shapes that only slightly depart from a truly spherical form (but which may still be described as having a single geometric length dimension), the shape effect on entrainment is minimal. However, for shapes which are essentially two dimensional, the orientation of grains in a sedimentary bed has considerable effect. Although there is no information available concerning the entrainment of leaves, Schoklitsch (1914), Shields (1936) and Pang (1939) have all investigated the entrainment of flaky solids. The first two authors consider that flaky solids move at fluid stresses higher than those necessary to entrain granular solids, whereas Pang (1939) comes to the opposite conclusion. The cause of their disagreement may well be in the different initial orientations of the plates in their sediment beds which were artificially laid (P. Mantz, pers. comm.). Mantz (1973) carried out similar experiments, but using a naturally laid mixed sediment bed, and found that the entrainment of fine-grained flaky solids occurred at fluid stresses less than those required to move granular solids with the same fall diameter. Clearly, if leaves behave similarly, then considerable sorting would result, purely on the basis of shape, between, for example, leaves

and fruits. It should be noted, however, that all workers have so far used plane sedimentary beds (defined as plane to within one solid particle diameter), a condition that rarely exists in nature.

The effect of leaf orientation and aspect with regard to the fluid flow clearly determines the critical fluid stress at which the leaf will begin to move. Elongated objects, such as twigs, tend to remain stable at fluid flows of greater magnitude when they are aligned parallel to the direction of flow, and this effect is sometimes observed in fossil deposits. Such a condition arises because in this orientation the object presents a smaller area to the fluid flow, therefore the fluid stresses experienced by the object are low, thus movement only begins at correspondingly higher fluid flow.

Many fluid dynamics equations require that an effective geometric dimension be ascribed to the sedimentary particle under investigation. With a sphere such a dimension is the diameter. It is, however, clearly impossible to directly ascribe such a length dimension to a two dimensional object, such as a leaf, since the effective value of this parameter will vary with the orientation of the leaf to the fluid flow. The fluid flow, in turn, will affect the orientation of the leaf as is illustrated in Fig. 51. The effect of the turbulent wake is to impart instability to an unfixed plate,with the result that its orientation with respect to the fluid flow is continually changing. Such a condition may be observed in leaves falling in still air, hence the empirical approach adopted in chapter 10. If the terminal velocity of a leaf is such that a turbulent wake is produced, then the leaf will flutter or spin to the ground, in spite of the attitude at which it begins to fall or turbulence in the surrounding air. The natural variation in size and shape, as well as the flexible nature of leaves, makes assigning a characteristic

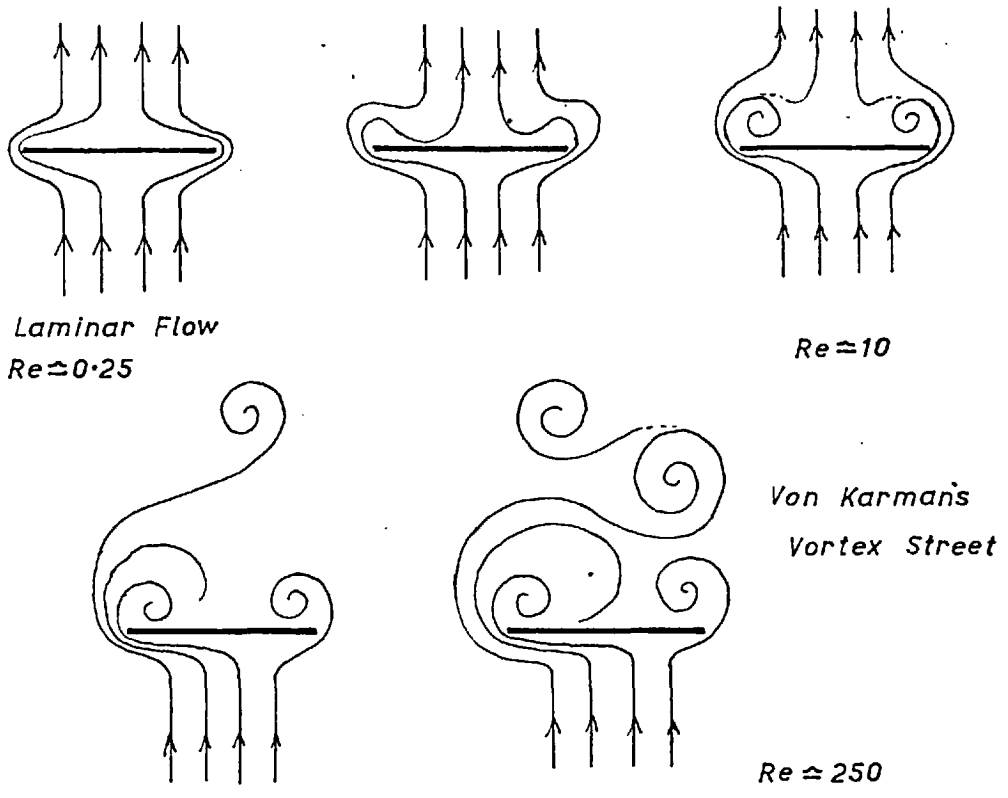


Fig. 51. A rigid plate is held normal to a fluid flow. As the Reynolds number (below) is increased, which in this case is achieved by increasing the flow past the plate, eddies form in the lee of the plate. At first these eddies are small and symetrical, but as the fluid flow is further increased the eddies become unstable so that at high Reynolds numbers a series of unequal eddies stretch along the wake behind the plate. (After Batchelor, 1967, plate 4).

The Reynolds number is a dimensionless number which may be interpreted as being proportional to the ratio between inertial and viscous forces. It is given by

$$Re = \frac{UL\rho}{\mu}$$

where U is the velocity, L is the reference length, ρ = density and μ = dynamic viscosity.

length impossible, thus even under ideal conditions, where fluid turbulence is at a minimum, the behaviour of leaves cannot be described by simple equations of fluid dynamics.

The settling of leaves in water is more complicated. As leaves tend to become saturated the density of the leaf will alter, not only with time, but also from place to place within the leaf. Furthermore, the deposition of sediment particles on the surface of the leaf, and invasion of the tissues by microorganisms, will also affect the density.

Mantz (pers. comm.) has suggested that for flaky solids the nominal diameter might be used as an approximation to a suitable characteristic length. This measurement is the diameter of a sphere of equal volume to that of the flake. However, data from mineral solids approximating to spheres indicates that transport behaviour cannot be achieved better than to within one order of magnitude, thus similar predictions for leaf transport may be greatly in error.

In spite of the difficulties of theoretically describing individual leaf/fluid interactions, the effect of hydraulic sorting of leaf populations may be strong enough to produce characteristic patterns of assemblage structure which may prove useful in determining the relative growth positions of the component species.

The concept of hydraulic equivalence may also be utilized to determine the predominant transport medium of various species in relation to the entombing sediment, and thereby distinguish source areas. Two particles are said to have the same hydraulic equivalence if they react similarly to a given set of fluid stresses. Thus, if two sediment grains come to rest side by side in a sediment bed that

is being deposited under a field of gradually decreasing fluid stresses, such as on an ideal* delta front, then they are said to be hydraulically equivalent. If it is supposed, for the moment, that stream waters, on entering a lake flow over the delta slope with a gradually decreasing velocity, leaves will be deposited along with sedimentary grains of the same hydraulic equivalence, at positions on the delta front that reflect their hydraulic characteristics. This will result in considerable sorting. By comparison, on the lake bottom where the fluid stresses are negligible, the sunken leaves will exhibit a wide range of hydraulic characteristics.

If a population of fossil leaf remains is considered to have the same hydraulic equivalence as the sediment grains composing the surrounding matrix, then it is extremely likely that both were deposited in response to the same fluid medium. Under certain circumstances, therefore, it may be possible to isolate the transport medium for a particular group of remains, and thereby gain a clue as to the species distribution within the source vegetation.

From the afforegoing discussion it is unlikely, however, that the hydraulic characteristics of plant remains can be theoretically deduced. An empirical approach might well be more promising.

* Such a situation is unlikely to obtain under natural freshwater conditions since stream waters, on meeting the relatively static lake waters of similar density, undergo a sudden loss of energy through turbulent mixing.

RELATIVE DEPOSITION RATES OF LEAVES AND SEDIMENT

In all fossil plant deposits (except those resulting from peat accumulations) the plant remains are closely associated with inorganic sediment grains to some degree or another. Variations in the concentration of leaves relative to sediment are used as a basis for distinguishing between assemblages or palaeosuccessions (Krassilov, 1969). However, these fluctuations in the plant concentration may not necessarily be a function of the source vegetation, and therefore the restriction of an investigation to well defined plant beds may only give limited palaeoecological information. As a preface to considerations of sampling in fossil plant deposits it is pertinent to examine the plant/matrix depositional relationships in more detail.

The rate of leaf deposition, R_L, at any point on a sedimentary surface may be expressed thus:

$$\text{Rate of leaf deposition } R_L = \frac{\delta L}{\delta t} \qquad (1)$$

L represents some measure of the amount of leaf material expressed as numbers, volume or mass deposited in a small time interval t. If t is small enough the rate of leaf deposition may be regarded as constant. Similarly, the sediment deposition rate, R_s, may be expressed thus:

$$R_s = \frac{\delta s}{\delta t} \qquad (2)$$

where s is a measure of the amount of sediment deposited during time t. If s and L are measured in the same units an index of leaf concentration, K, within the sediment may be expressed as the leaf/sediment ratio:

$$\frac{R_L}{R_s} = K \qquad (3)$$

This expression may be expanded to include the leaves from the

various component species (a, b, c ... n) of the source vegetation

$$\frac{R_{La} + R_{Lb} + R_{Lc} \ldots . R_{Ln}}{R_s} = \frac{\sum_1^n R_{Ln}}{R_s} \qquad (4)$$

The fossil leaves on a rock surface exposed by splitting along the bedding plane represent, assuming no post burial losses, those leaves deposited in a small time period, and any lateral variation in component species, or leaf abundance, is indicative of differing sedimentation rates of either leaves or sediment over that depositional surface.

A vertical section through a horizontally bedded sedimentary pile containing fossil leaves presents a series of bedding planes varying in leaf densities. Depending on the thickness of the rock investigated, these vertical densities represent deposition over considerably longer time intervals than have so far been investigated. As the time interval, t, increases, so does the probability that the deposition rates of either leaves, or sediment, will not remain constant. Under these conditions expression (1) becomes:

$$L = \int_{t_o}^{t_z} \left(\frac{\delta L}{\delta t} \right) t$$

or

$$L = \int_{t_o}^{t_z} R_L \delta t \qquad (5)$$

and similarly expression (2) becomes:

$$s = \int_{t_o}^{t_z} R_s \delta t \qquad (6)$$

by integrating between time t_o and time t_z; the beginning and end of the depositional period.

Clearly the smaller the interval $t_z - t_o$ is, the better the

resolution obtainable in the analysis of the deposit. In order to obtain the best resolution, and to ensure sedimentation rates were more or less constant, volumes of sediment may be delimited by utilizing the sedimentation unit concept proposed by Otto (1938). The sedimentation unit at any point is defined as "that thickness of sediment which was deposited under essentially constant physical conditions". Thus, by definition, if such a thickness of rock is sampled the relative rates of leaf and sediment deposition should have remained constant during the period of deposition, and no loss of resolution will be incurred due to sampling. In practice the sedimentation unit may be difficult to define, consequently values of K would only represent approximations.

Two possible sources for the variation of K between samples may be determined. The primary source of variation must come from the differing physical conditions of hydrodynamics, sediment type and availability etc. that define the sedimentation unit. For leaves that are being transported by the same medium as the inorganic sediment grains these conditions will determine sorting which will inherently affect the value of K.

A second cause of variation is the source of the leaf material which is, of course, dependent on the distribution of the source vegetation. This may lead to a fluctuating value of K even though the physical conditions of deposition of the inorganic sediment matrix may be constant.

The problem of distinguishing between these two components of variation is a major obstacle in the analysis of past vegetational regimes. Yet by careful analysis of the three dimensional patterns of deposition in a deposit, this problem may sometimes be overcome.

SAMPLING FOSSIL ASSEMBLAGES

The main objective of any sampling is to derive as much information as possible about the sampled population in the most economical way. When sampling fossil plant assemblages the sampled population is the complete population of fossils within a rock unit and, using the nomenclature adopted by C.R. Hill (1974), this fossil population may be termed the 'Target population I'. By describing the parameters of this population as accurately as possible it is hoped that some information about the original source vegetation communities will be derived. The population of individuals comprising the source vegetation will be known as 'Target population II'.

The degree of accuracy achieved in describing the Target I population will clearly depend on the nature of the sampling methods, and any conclusions arrived at concerning the Target population II are dependent on the quality of the estimate of the Target I population parameters.

In the course of the development of quantitative plant ecology numerous sampling regimes and methods have been devised to efficiently estimate factors of floristic importance from vegetational communities. However, the nature of the rock matrix, combined with the three dimensional structure of a sedimentary deposit, imposes certain restrictions on the sampling methods that have been developed in connection with phytosociological studies.

The condition that a set of quadrats (or sample stands) should be distributed within a sample area (or volume) in such a way that each quadrat is independent of all the other quadrats, as well as any structure within the sampled community, cannot always be met when sampling fossil plant assemblages for the following reasons:

a) The amount of material, within the total deposit, available for sampling.

The fact that any deposit is exposed for sampling by the palaeo-ecologist is usually the result of partial removal of the original fossil population. The initial exposure is often made by nautral erosion, e.g. coastal cliffs, stream sides, etc., but may also be the result of activities by man; quarries or road cuts.

Similarly, some of the deposit may be inaccessible because it is covered by large amounts of other rock in the form of scree, fallen boulders or slumping.

b) Weathering

Of the accessible deposit, large areas may be differentially weathered which may lead to the selective destruction of some of the component fossil species.

c) The splitting properties of the rock matrix

Clearly any sedimentary rock that cleaves parallel to the bedding will favour the exposure of entombed fossils since most remains are deposited, or distorted by compaction, so that their plane of largest area is parallel to the bedding surface. A large number of variables affect the splitting properties of rocks including the presence of organic remains themselves.

d) The quality of bedding

This will greatly influence the splitting properties of rocks and is determined by such factors as grain size, grain shape and orientation, sedimentary structures and rock chemistry.

In all but the most homogeneous deposits the above factors will largely determine the sampling regime, and, since pattern (which is what

we are trying to detect) is by definition the result of heterogeneity, true random sampling of a three dimensional deposit can rarely be achieved. Thus the statistical methods employed to determine pattern must be either robust or non parametric. Fortunately robustness is a quality of many multivariate techniques such as Principal Components Ordination or Reciprocal Averaging.

As regards sample size, the criteria used in phytosociological studies are equally applicable to the fossil situation.

Stand size

In plant ecology the size of stand is primarily determined by scale within the vegetation and this is just as important in the analysis of fossil plant assemblages.

The construction of a species-area curve in order to determine a suitable stand size (see Greig-Smith, 1964 pp 151-155 for relevant discussion) has to be based on the portion of the sample population immediately available at the start of sampling, but this estimate of stand size may not be suitable for sampling all parts of the fossil population.

The effect of pattern within fossil situations may also greatly influence the choice of size for the minimal or representative quadrat area. "Both the scale and intensity of pattern of the different species will affect the size of minimal area found, if, indeed, any definite area can be determined. A species will appear at a relatively small size of quadrat if the only pattern it exhibits is small scale. If large-scale pattern is present, the size at which it appears will depend on its intensity: a species with dense clumps, separated by spaces in which it is absent ..... will tend to appear

only in large quadrats. Conversely, a species with large-scale pattern of a mozaic of patches with higher and lower density ..... will appear at a smaller quadrat size." (Greig-Smith, 1964, p155).

Large variations in fossil density between adjacent quadrats have been noted by C.R. Hill (1974). Such a situation is likely to obtain in most, if not all, fossil plant beds laid down under anything but the most uniform conditions and work at Hasty Bank, carried out by C.R. Hill, has shown that one's choice of stand area, or volume, may in fact have to change with differing lithologies, fossil density and fragment size.

Three dimensional sampling

The analysis of the distributions of plant remains over a single bedding plane is analogous to investigating vegetation pattern over a land surface, since both may be assessed using a two dimensional sampling regime. It may be supposed therefore that subsequent three dimensional information about a deposit may be obtained by sampling successive bedding planes.

Once again, however, practical considerations limit the approach. In the first instance the concept of a bedding plane is not immediately conducive to this type of sampling since it may not have any physical expression, and thus sampling over large lateral distances would inherently involve the possibility of sampling across different bedding surfaces.

Secondly, the orientation of plant remains may not be parallel to the bedding, consequently the stand must become three dimensional in order to adequately recover these remains for identification. This in turn may disturb underlying bedding planes resulting in the breakdown of the sampling regime.

Thirdly, the splitting properties of the matrix may preclude the exposure of planar stands of sufficiently large area, consequently the excavation of a finite thickness of rock is inevitable.

The necessity for sampling volumes rather than areas introduces further problems. The extension of the boundaries of a stand in a direction normal to the bedding introduces the likelihood of that stand including individuals that were laid down under changing depositional conditions. To overcome this problem it is necessary to utilize the sedimentation unit concept proposed by Otto (1938) which was defined as "that thickness of sediment which was deposited under essentially constant physical conditions." The words "essentially constant" do not however preclude the existence of a trend, which may be linear or cyclic, and includes chance deviations of all sedimentary characteristics about a mean value. Thus heterogeneity in the floristic components between laminae within a sedimentation unit is allowed for. Providing individual stands do not cross sedimentation unit boundaries they will represent samples of sediment laid down under uniform conditions. The criteria for identifying these boundaries are given in Otto's paper.

The abundance of fossil plant remains within any unit of rock has already been shown to be largely dependent on the deposition rate of plant matter in relation to that of the matrix. Examination of these variations in leaf concentration within sedimentation units may yield floristically important information and this will be discussed further later. However, it should be pointed out that the presence of large amounts of organic matter or mineralized plant remains within the matrix will influence its splittability, and hence affect the sampling.

After deposition a sedimentary pile will become compacted. This increases the abundance of plant remains per unit volume of rock. If compaction is uniform it has little consequence, but such a condition is rarely fulfilled. The degree of compaction is more likely to differ from place to place throughout the deposit such that the relationship of fossil abundances between stands becomes distorted. Obviously, under these circumstances, any statistical procedure that is susceptible to varying inter-stand abundances in the derivation of floristic ordinations, such as principal components analysis (discussed on page 169), should not be used.

Quantitative assessment of abundance

Unless presence or absence data is to be used some measure of abundance of individuals within stands must be attempted. The two measures used in phytosociology that are applicable to fossil plant assemblages are density and cover, and these may be defined thus:

Density - A count of the number of individual fossils, whether representing whole or fragmented organs or organisms, that occur within a sample stand.

Cover - The proportion of a planar stand area, aligned parallel to the bedding, that is occupied by a normal projection on to it of the individuals representing a species that occurs within that stand.

Both these definitions refer to the potentially measurable paramenters of the Target population I. The success of achieving an accurate assessment of density (or cover) of species occurring in the target population I is dependent on characteristics of the sampling method as well as the rock matrix.

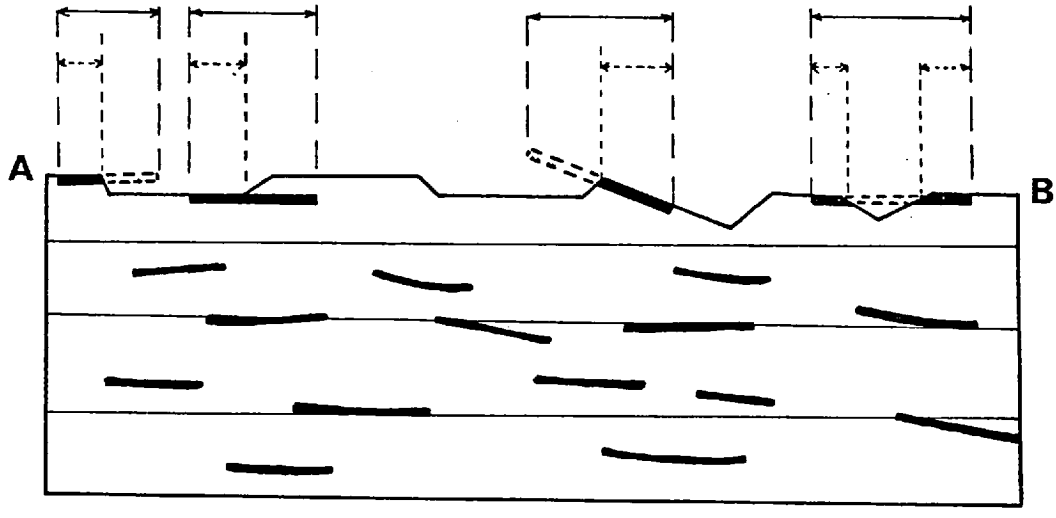


Fig. 52. A schematic representation of a vertical section through a three dimensional sample stand. A-B represents the best exposure of a bedding plane that could be achieved by splitting. The leaves, shown in section, have clearly influenced the splitting along A-B, but have become fragmented in the process thus density and cover estimates both give erroneous assessments of abundance: density over-estimates abundance and cover under-estimates abundance.

To demonstrate this let us consider Fig. 52 which is a diagrammatic representation of a vertical section through a three dimensional sample stand. The upper surface represents the best exposure of the bedding plane A-B that could be achieved by excavation and splitting. Clearly recovery will depend on the splitting properties of the rock matrix and the influence on this by the incorporation of the fossil material. It can be readily seen that the actual number of leaves originally lying within the rock close to this plane was four. However, fragmentation of the leaf on the extreme right leads to the exposure of five pieces of material and thus, in this particular case, a 25% over estimate of density might be made. If cover estimates were attempted, using, for example, point quadrats (see Goodall, 1952), and it was possible to measure the exposed pieces of leaves by this method without any errors, there would still be an underestimation of cover by 50 per cent. The complete exposure of fossil leaves, necessary for accurate cover measurements, is rarely, if ever, achieved which results in an inevitable underestimation of the Target population I cover abundance.

By contrast density may, if excavation or splitting of the stand surface is not carefully carried out, lead to a potential over-estimation of abundance.

Another problem of measuring cover abundance is that many of the more practical methods of assessment, such as point quadrats, are in themselves only able to <u>estimate</u> the exposed cover since the rationale behind them is of a statistical nature. Recording the number of individuals exposed on a rock surface is, on the other hand, a more direct measure but can be rather tedious when the concentration of plant material is high.

It is clear that although cover and density are both measurements of abundance, they measure different properties of the population, and the meaning of either of them, or the relationship between them, is obscure. The presence within a stand of an individual, whether it be a whole leaf or a fragment, represents a discrete depositional event that took place along with the other depositional events of the inorganic sediment grains. Consequently, density is related to the processes of sedimentation that characterize a particular depositional environment. It is likely therefore that throughout a deposit, and particularly vertically, variations in plant density will be associated with variations in lithology.

Cover, on the other hand, is predominantly controlled by morphology. A locally abundant plant X, producing large tough leaves, will tend to have a more uniform cover abundance score from those stands in which it occurs than, for instance, a similarly abundant pteridophyte Y with a large number of small fragile pinnules. Species X will always have a high cover rating from those stands in which it occurs. Species Y, however, will exhibit a wide range of cover abundances depending on how many pinnules are present within the stands. Throughout the deposit species Y must be present in greater numbers than X even to equal the cover score for X.

It might be assumed that this characteristic of some species components being less variable from stand to stand provides more suitable data for principal components ordination (for reasons discussed on page 169). However, this feature merely reflects the morphological influence inherent in cover abundance estimates and there is a danger that it would invalidate any floristic pattern derived from the ordinations.

C.R. Hill (1974) has observed "The extent of fragmentation of

fossil leaves ..... varies tremendously from sample to sample and for this reason abundance counts (density) can scarcely be expected to reflect directly the real proportions of the whole leaves deposited in the plant bed. Even less can they be expected to reflect the proportions produced by the different species when they were alive." Hill suggests that theoretically at least this information might be better provided by estimating 'cover' in the fossil assemblage. However, he then comments that the fragmentary nature of many fossil forms, as well as the frequent lack of extant relatives, prevents such parameters of the ancient community from being reconstituted even from cover data.

The result of the delta trap experiments shows that long distance aerial transport sorts in favour of small leaves (Figs. 22 and 23). The selection of small leaves by aerial transport, which results in the biassed representation of certain components of the source flora, immediately invalidates cover as an abundance measure since species predominantly transported to the depositional site by wind will, overall, have a lower abundance score.

A similar argument may be advanced against the use of density measures in that fragmentation is dependent not only on the species of leaf, but also on the distance and length of time it is transported prior to deposition.

While there are clearly arguments both for and against the use of either measure, it would seem that from consideration of the large potential errors involved in the estimate of cover, the morphological bias, and the problems of relating cover estimates to parameters of the source vegetation, density is a more suitable measure of abundance.

PRINCIPAL COMPONENTS ORDINATION AND RECIPROCAL AVERAGING

Multivariate statistical techniques such as Principal Components analysis (P.C.A.) and Principal Coordinates analysis (Gower, 1966) have been used for some time in phytosociological studies e.g. Orlóci (1966). PCA has proved particularly suitable for investigating dependence structure that might occur within a suite of observations on vegetation where no pre-existing patterns are suspected. Unlike classification techniques, such as association analysis, principal components ordination does not force the data into what may be entirely false groupings where no discontinuities in the data exist. Although normally presenting a continuum that might be assigned, by inspection for example, to an environmental gradient, it will detect discontinuities, and thereby group the data, if such a clustering is justified. The clustering thus produced by PCA may then be used as a basis for dividing the sampled vegetation into communities each exhibiting a more homogeneous structure. In spite of a theoretical requirement for homogeneity, PCA, like many other multivariate statistical methods is remarkably robust and will still give a fair result on data not fulfilling this premise. This robustness allows application of such methods to the analysis of fossil plant distributions, where sampling may be subject to constraints of exposure and lithology, and where the distribution of individuals may depart from normality.

In simplified terms principal components analysis may be thought of in the following way. If only two species were present in the sample population the occurence of these species within a stand (quadrat) would define the position of that stand on a two dimensional graph with the axes representing some quantification of the two species. Similarly, if three species occurred then a three dimensional graph

could be constructed. Although impossible to visualize, the same procedure can be mathematically expressed for any number of species and any number of stands, with the result that a swarm of stands (or if stands are used as the axes, species) conceptually exist in multi-dimensional hyperspace. This only begins to have understandable meaning if the distribution of stands or species can be summarized by projection on to three dimensions or less, but this unfortunately introduces distortion. This distortion may be minimized if the projected axes are aligned with the major axes of variation within the multidimensional scatter. PCA, therefore, is a method of detecting these principal axes, or components of variation, in data matrices of apparent homogeneity.

The implication of the graphical analogy is that the extracted axes of variation are orthogonal. This may not represent their true relationship, but this does not invalidate the technique for ordering the data. Orthogonality in PCA, and other truly multivariate analyses, plays exactly the same role as it does in univariate analyses; namely the preservation of the statistical independence of the components of variation (Blackith and Reyment, 1971).

The above discussion was presented primarily in terms of a stand ordination based on species as attributes, and a technique carrying out such an ordination is known as a Q technique. Alternatively, R techniques ordinate species in terms of the stands in which they occur. Although the methods are, to some extent, interchangeable the principal components of the R matrix are not the same as the principal axes of the Q matrix when unstandardized data is used. If, however, the data is appropriately standardized, the two calculations become rearrangements of one another (Blackith and Reyment, 1971, p.210).

Standardization

Standardization is a widely used technique of transforming the data to allow comparison of variables which have been measured in different units. The transformation of the raw data matrix (a variance-covariance matrix) is achieved by subtracting from each observation the mean of the data set and dividing by the standard deviation. In this way a new matrix is derived (a correlation matrix) in which the variables have a mean of zero and a variance of one. Such a procedure reduces the overall variance in a set of observations and gives equal weighting to all variables. Standardization 'adjusts' certain components of the data more than others e.g. those species with a high variance are divided by a correspondingly high standard deviation. Clearly, such adjustment may not always be desirable. However, differences in abundance between stands, which cause fluctuation in variance, may be brought about by factors other than those of direct palaeobotanical significance; for example differential compaction, and under such circumstances standardization could be acceptable.

Another way of reducing the overall variance in a data set is by means of a logarithmic transformation. The usefulness of this procedure, which does not alter the relationship between species (or stands), will be examined later.

Presence and absence data

If presence and absence data were used in the ordination the effects of compaction would be minimized but, unfortunately, such a data matrix would contain little information of palaeobotanical significance. This is because the large number of interacting variables operating on plant remains at deposition, tend to produce an apparent homogeneity in the distribution and produce a seemingly large

'random' element. This would be especially evident in lateral distributions over single bedding planes. Because of the extensive mixing, the presence or absence of the common species in a quadrat may not be very meaningful and the ordination would have to be carried out on the basis of the distribution of the rare species alone. Clearly, such an approach is intuitively erroneous. The nature of the fossil population, therefore, necessitates the collection of quantitative rather than qualitative data.

P.C.A. ordination of the Silwood delta surface data

Leaf fragment abundance data from the surface sediment of the Silwood delta (see Fig. 9 for sampling positions) was analysed by a Q type principal components ordination using both unstandardized data and data that had been standardized to unit variance. The computer program (Q.P.C.A.) was written by Dr A. J. Morton of Imperial College. It is based on an iterative procedure (Lawley and Maxwell, 1963) and operates on a half matrix to reduce core space.

Fig. 53, the plot of the unstandardized principal component ordination shows a tight bunching of the majority of the stands to the left of the plot. Reference to the raw data (Appendix table 1) shows all these stands to have relatively low species abundances. It has been pointed out by Orlóci (1966) that species rich assemblages differ in more species than species poor assemblages, and that where there are significant numbers of species poor stands, these will ordinate close together with respect to the more species rich stands. Indeed in Fig. 53 the stands plotting apart are those with high species abundances. Thus axis I appears to reflect variation due to abundance. Such an observation is not new, and indeed is common in PCA ordinations. Axis II, however, may be assigned, by inspection,

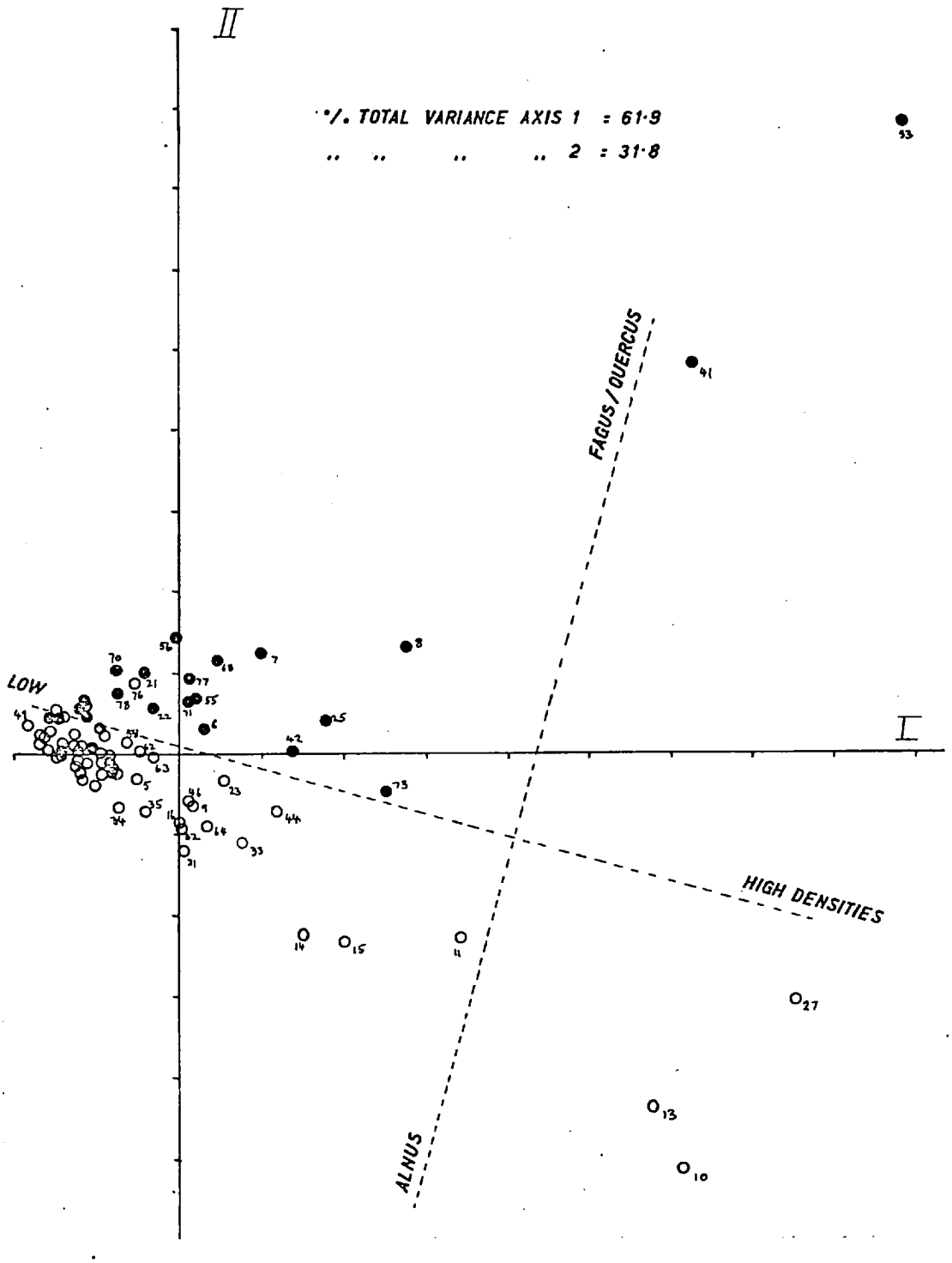


Fig. 53. Axes I and II of a Q type principal components ordination of 9 species of leaves occurring in the Silwood delta sediments. The ordination was based on unstandardized fragment density data. The numbers refer to the quadrat numbers (see Fig. 9) and the solid circles are those quadrats belonging to the Fagus/Quercus group as identified by Reciprocal Averaging (Fig. 56).

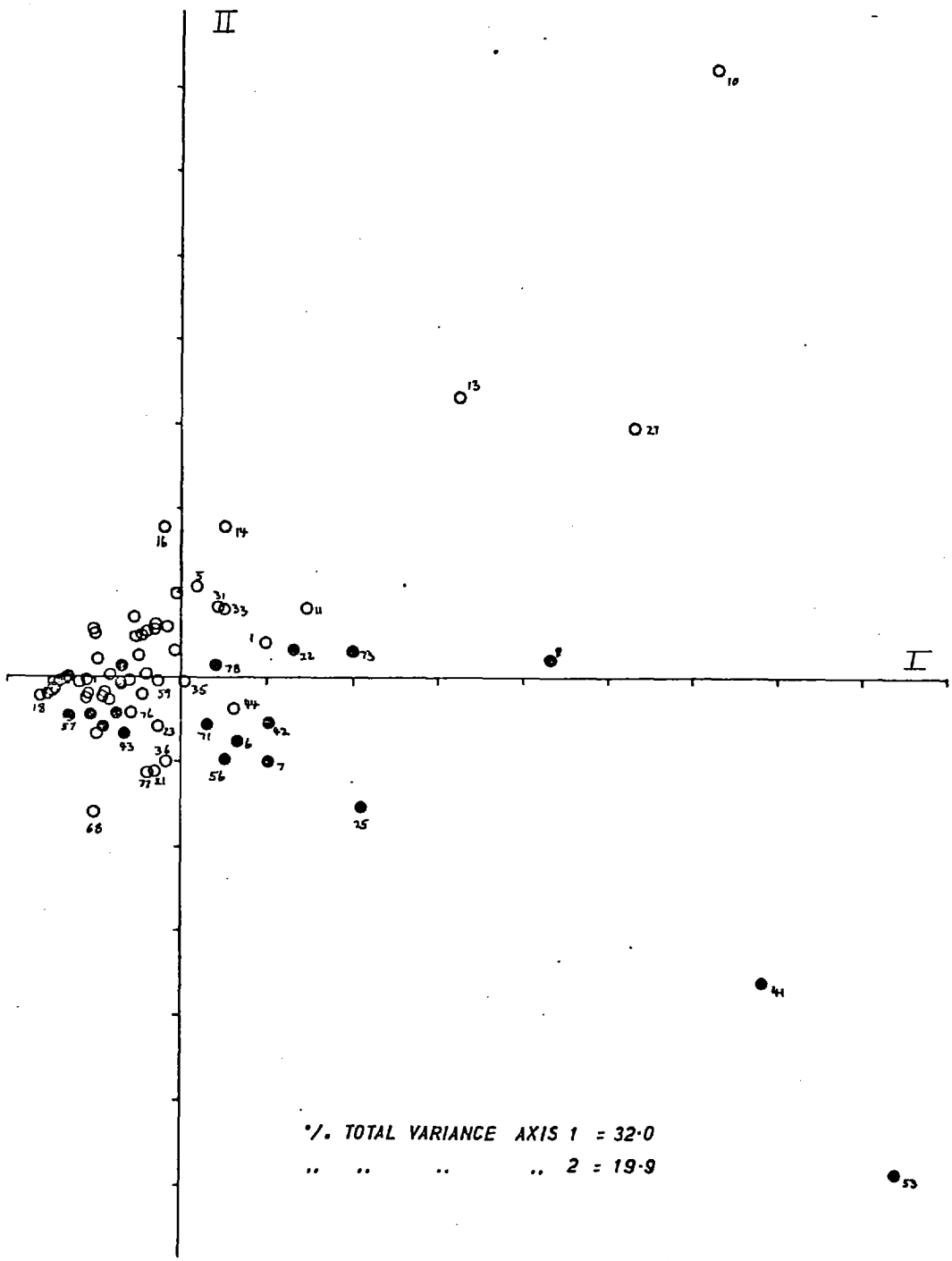


Fig. 54. A similar ordination to Fig. 53, but based on data standardized to unit variance.

to reflect a trend from proportionately high Alnus abundances to proportionately high Fagus/Quercus abundances.

The standardized data ordination, Fig. 54, seems to be little different from that obtained from unstandardized data. Axis I is again aligned along an axis of abundance while axis II again reflects ordering from proportionately high Alnus abundances to proportionately high Fagus/Quercus abundances. It is worth noting, however, that the total variation accounted for by the first two axes of the unstandardized data ordination was 93.7% while that for the standardized was only 51.9%. Thus in this instance standardization has reduced the effectiveness of the ordination. Both ordinations have identified, on axis II, an axis in the data along which stands may be ordered in terms of the relative abundances of Alnus or Fagus and Quercus, but the lack of any discontinuities within the data does not facilitate mapping the delta in terms of two, or more, discrete regions displaying, within themselves, more or less homogeneous species compositions.

Successful as PCA ordinations are in presenting such trends, the method itself suffers from a number of drawbacks. Unstandardized PCA ordinations are not corrected for species abundance which results in the rarer species having a smaller axis score even though their distributions throughout the sampled population may be similar. This introduces problems when dealing with fossil form genera that may have been only parts of a single living entity. Naturally occurring associations between organs would not be detected since, for example, flowering parts would be considerably rarer than leaves.

In a Q type analysis this characteristic of PCA has even more disturbing consequences. If the abundance of fossils within a unit volume of rock is noted, and this data is subsequently ordinated using PCA, spurious results may be introduced due to the effect of varying

abundance scores arising from differential compaction during fossilization rather than any vegetational or depositional variables.

Another problem with PCA ordinations is that they are not particularly suitable when it becomes desirable to use fossil forms as stratigraphic indicators. The variation of fossil species, both within and between different lithologies, may be dependent on a number of controls, and these are obviously important when considering relationships between the fossil assemblage and the living community. Thus it becomes important to relate any structure within a stand ordination to those species characterizing the various parts of that structure and the absence of any direct relationship between stand and species ordinations arising from PCA makes this process somewhat complicated.

Reciprocal Averaging

Reciprocal Averaging described by M.O. Hill (1973) is an eigenvector method of ordination somewhat akin to PCA ordination that overcomes the problems outlined above. Although it may be thought of as operating in a similar way to PCA its rationale is developed from a different standpoint. The following is based on Hill's paper: A species (row) by stand (column) matrix is constructed and an arbitrary set of species starting scores, between 0 and 100, is produced. This should in practice reflect what is suspected as being the main gradient of change, as a good initial choice reduces the amount of calculations required. Using this set of starting scores, a set of stand scores is obtained by averaging stand data in terms of the estimated species scores. These scores are then rescaled between 0 and 100. From this set of stand scores a new set of species scores is again derived, by averaging, and also rescaled between 0 and 100. This procedure continues back and forth until,

after a certain number of iterations (dependent on the initial species scores) the species and stand scores stabilize. The resulting vectors are a unidimensional ordering of the stands and species derived simultaneously from the data matrix. The second axis may be obtained by using a set of scores which were fairly near to the final scores of the first axis. These scores are then adjusted by subtracting a multiple of the first axis (see Hill's paper) and the iterations continued until a new set of scores stabilize. These become the second axis. The third and subsequent axes are derived similarly.

The simultaneous derivation of stand and species scores results in directly comparable ordinations. The species score is equal to the average stand score for those stands in which the species occurs (but rescaling so that the total range is 0 to 100), and the stand score, is equal to the average species score for those species which occur in the stand (but again rescaling between 0 and 100). This duality leads to the interpretation of a stand plot, in terms of the abundance of species within the stands, by simply overlaying the species plot onto the stand plot. Although there is a risk of circularity being introduced into the argument at this point, the species would not be used to interpret the stand plot in terms of causes of variation but only to characterize clusters, if they arise, from the ordination.

Hill makes the point that where there is a long floristic gradient it will always be presented linearly along the first axis of an ordination using R.A. whereas with P.C.A., "where there is a long and strong floristic gradient, stands which are extreme on the first axis of the ordination need not be extreme on the floristic gradient, and vice versa." (Hill, 1973). It should be pointed out also that the species scores derived by R.A. are corrected for species

abundance which is not the case with unstandardized P.C.A. ordinations; a rare species will usually have a smaller axis loading than a common species with unstandardized P.C.A. even though they may have the same distribution.

Hill also notes that with both P.C.A. and R.A. the second axis displays a quadratic dependence on the first axis and with R.A. this relationship applies to both stand and species ordinations. With P.C.A. the axes are orthogonal, but with R.A. the axes are not restricted to this condition even though they are so plotted for clarity.

It should be noted that the eigen value quoted for the axes on the R.A. ordination is not a measure of the variance extracted by the axes as given for the P.C.A. ordinations. Rather in R.A. it is a measure of the relationship between the stand and the attribute ordinations (M.O. Hill, 1974). Orlóci (1975) considers it as "an indication of the conceptual difficulty with which the quadrats can be ordered based on the species scores."

A Fortran IV computer program to carry out R.A. was written by Dr A.J. Morton based on the hand calculation method presented by M.O. Hill (1973). This program was subsequently modified by myself to generate three axes and to plot the resulting ordinations as figured in this thesis. The program is listed in the appendix.

RECIPROCAL AVERAGING ORDINATIONS OF THE SILWOOD DELTA SURFACE SEDIMENT DATA

The unconsolidated nature of the Silwood delta surface sediment facilitated the separation of whole leaves from fragments. It was therefore decided to treat fragments and whole leaves separately in order to determine the contribution made by each to any palaeoecological picture that might emerge.

Density Measures

The most straightforward estimate of leaf abundance is clearly a density measure and this will be dealt with first. Fig. 55 shows the attribute (species) plot obtained by R.A. of the fragment density per quadrat of the twelve taxa determined from the delta deposits. It can be readily seen that the majority of species lie along the top of the cube face representing the plot of axis 1 against axis 2. This depicts an ordination along axis 1 with all attributes having similar high scores on axis 2, except Nuphar which occurs in the bottom right hand corner. It appears, therefore, that Nuphar has a very different distribution pattern to any of the other species. Such a result is, perhaps, to be expected since, being an obligate aquatic only occurring in the lake, it is subject to different dispersal processes from all the other taxa. Indeed, the presence of Nuphar pads bearing beak marks in an apparently undisturbed delta leaf trap (Table 2) indicates that water fowl, as well as movements of the lake surface waters, may be responsible for some of its distribution.

Examination of the stand plot of the same ordination (Fig. 56) shows a similar crowding of stands with high axis 2 scores, the only exceptions being those stands containing Nuphar.

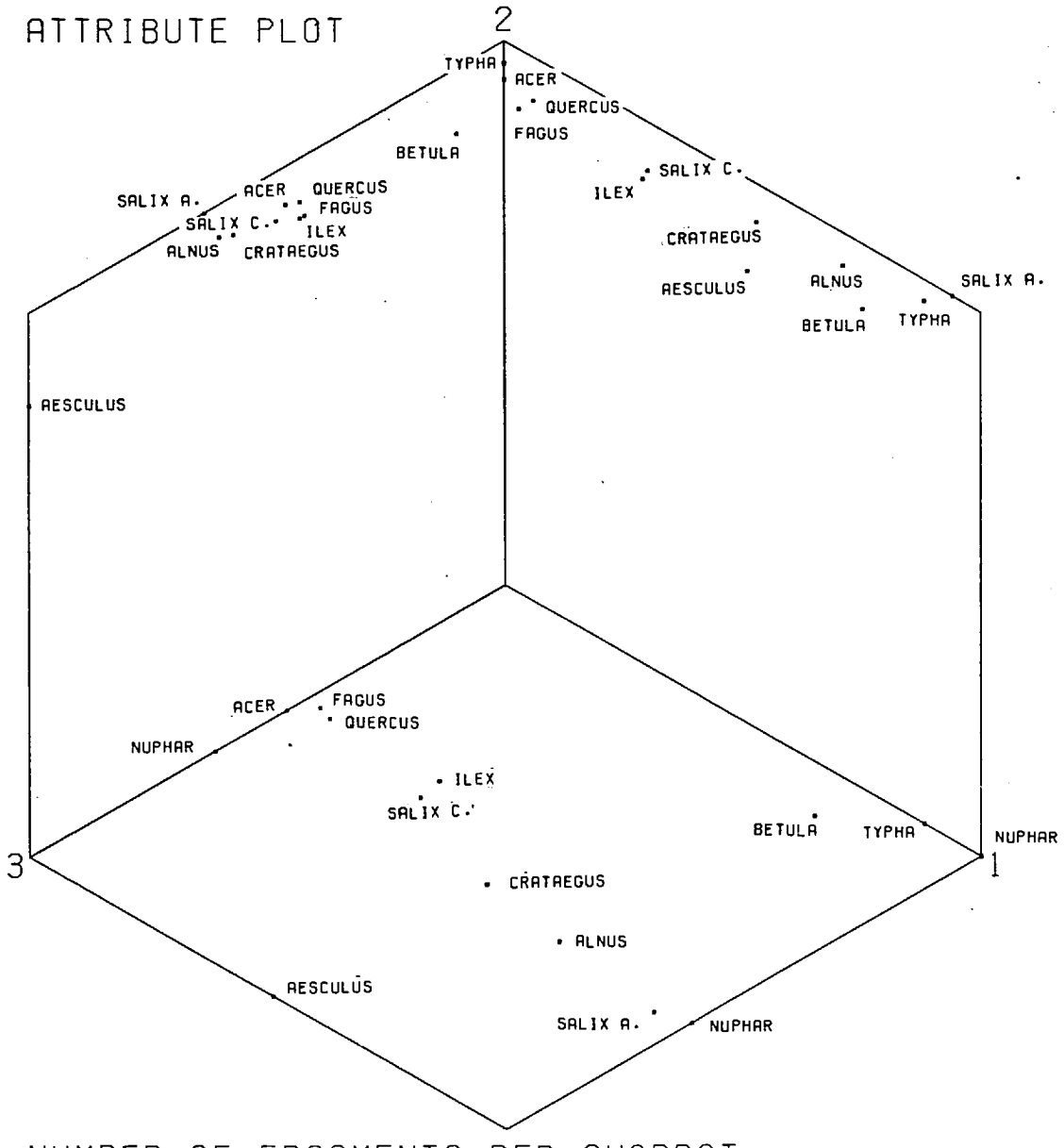


Fig. 55. Reciprocal Averaging ordination of fragment densities per quadrat as sampled from the delta surface sediment of Silwood Lake. In this plot twelve species are ordinated. The plots should be viewed as three internal faces of a cube on to which the positions of the species in three dimensional space have been projected. Thus, there are three times as many points in the total plot (above) as there are, in this case, species. The numbers 1, 2 and 3 at the corners of the plot denote the three axes originating from the centre of the diagram. Letters of the alphabet denote the number of points overlapping if this should occur, e.g. B ≡ 2, C ≡ 3, etc.

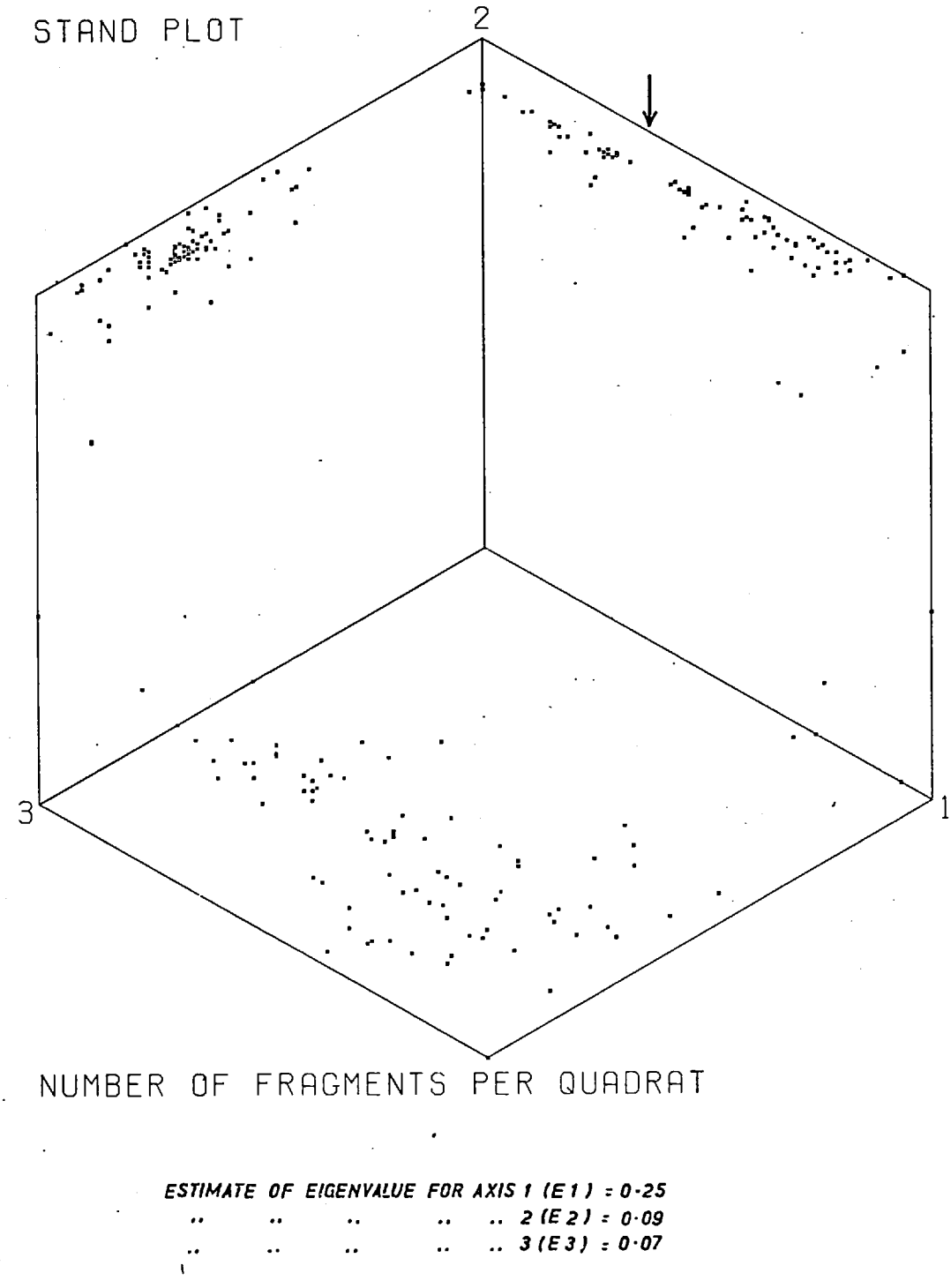


Fig. 56. The stand plot from the same ordination as in Fig. 55. A discontinuity in the ordination along axis 1 is marked by an arrow.

It is apparent that the ordination of stands along axis 1 is not continuous: there is a break at the position indicated by an arrow. By reference to the attribute plot (Fig. 55) we find that the group to the left of the arrow (consisting of stands 6, 7, 8, 21, 22, 25, 26, 41, 42, 43, 45, 46, 56, 57, 58, 59, 60, 62, 70, 71, 72, 73, 74, 76 and 77) is likely to be characterized by proportionately high densities of Acer, Quercus and Fagus with some Ilex and Salix cinerea. By contrast, the group to the right of the arrow (i.e. with higher axis 1 scores) is likely to contain proportionately high densities of Alnus, Betula, Typha and Salix alba with some Crataegus and Aesculus. By reference to the original data (Appendix Table 1) it is apparent that this is so. (Typha in this case probably also includes a small number of fragments of other monocotyledenous plants e.g. grasses).

Not all the 12 species ordinated here occur as whole leaves. In order to legitimately compare the ordinations of the fragments and whole leaf data, the fragment density ordination was again carried out using only those species that also occur as whole leaves. The resulting plots (Figs. 57 and 58) indicate that the ordination along axis 1 is essentially unchanged. With the removal of Nuphar, however, the axis 2 scores are completely altered. Removal of the 'constraint' imposed by Nuphar on the other species has led to a 'spreading out' down axis 2 and now the Betula distribution is shown to differ from the others. The dissimilarity of the Betula distribution was previously depicted on axis 3 of Fig. 55 along with that of Typha. It therefore follows that those species accounting for the greatest variation within the 'Alnus group' of Fig. 56 are firstly Nuphar, then Betula and Typha. The separation of Aesculus on axis 3 of Fig. 57 suggests that further variation is accounted for by the distribution of this species.

The discontinuity in the ordination on axis 1 of Fig. 58 is still

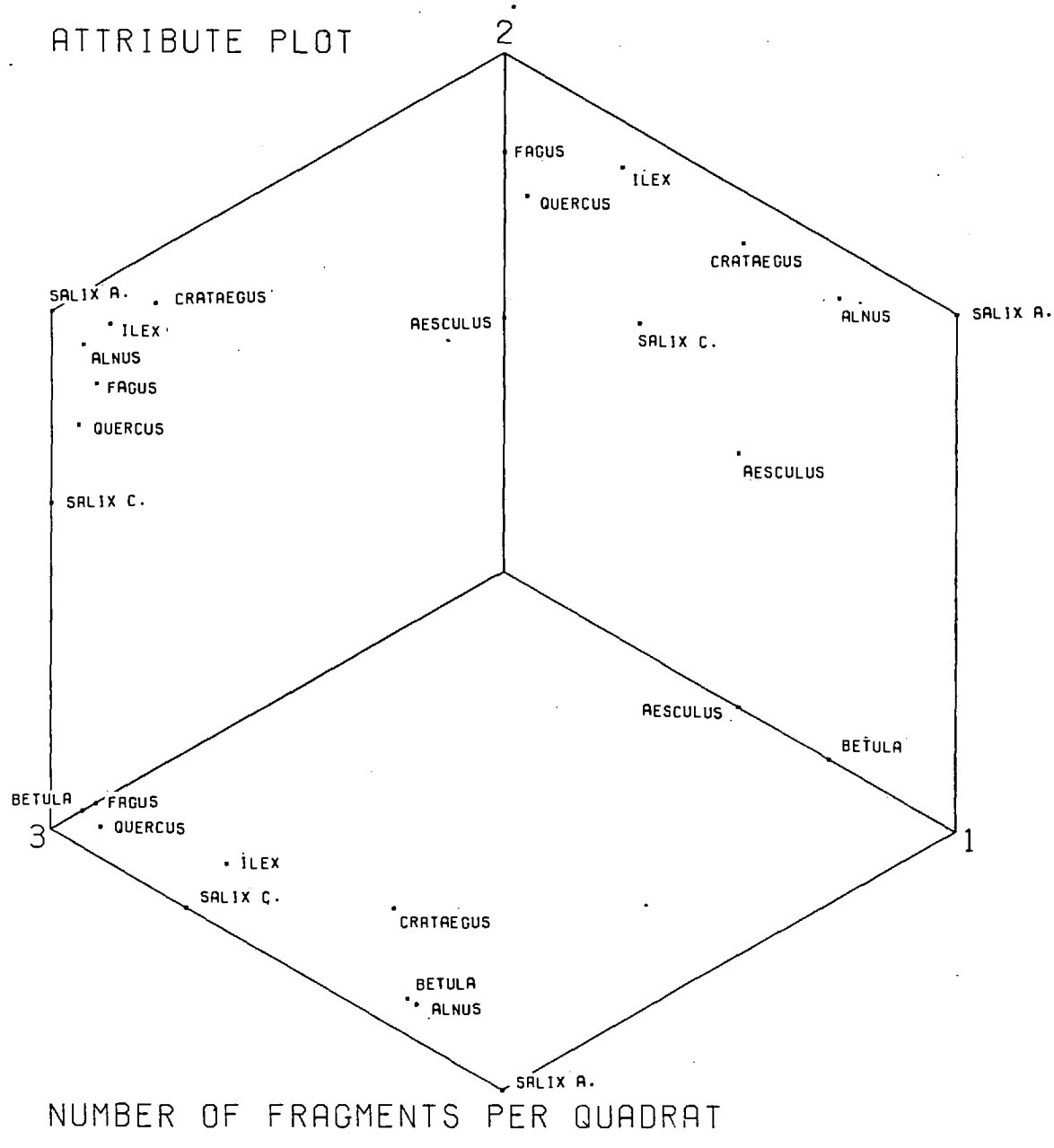


Fig. 57. Fragment density plot from the Silwood delta surface sediment. Nuphar, Typha and Acer density data were not included in the ordination.

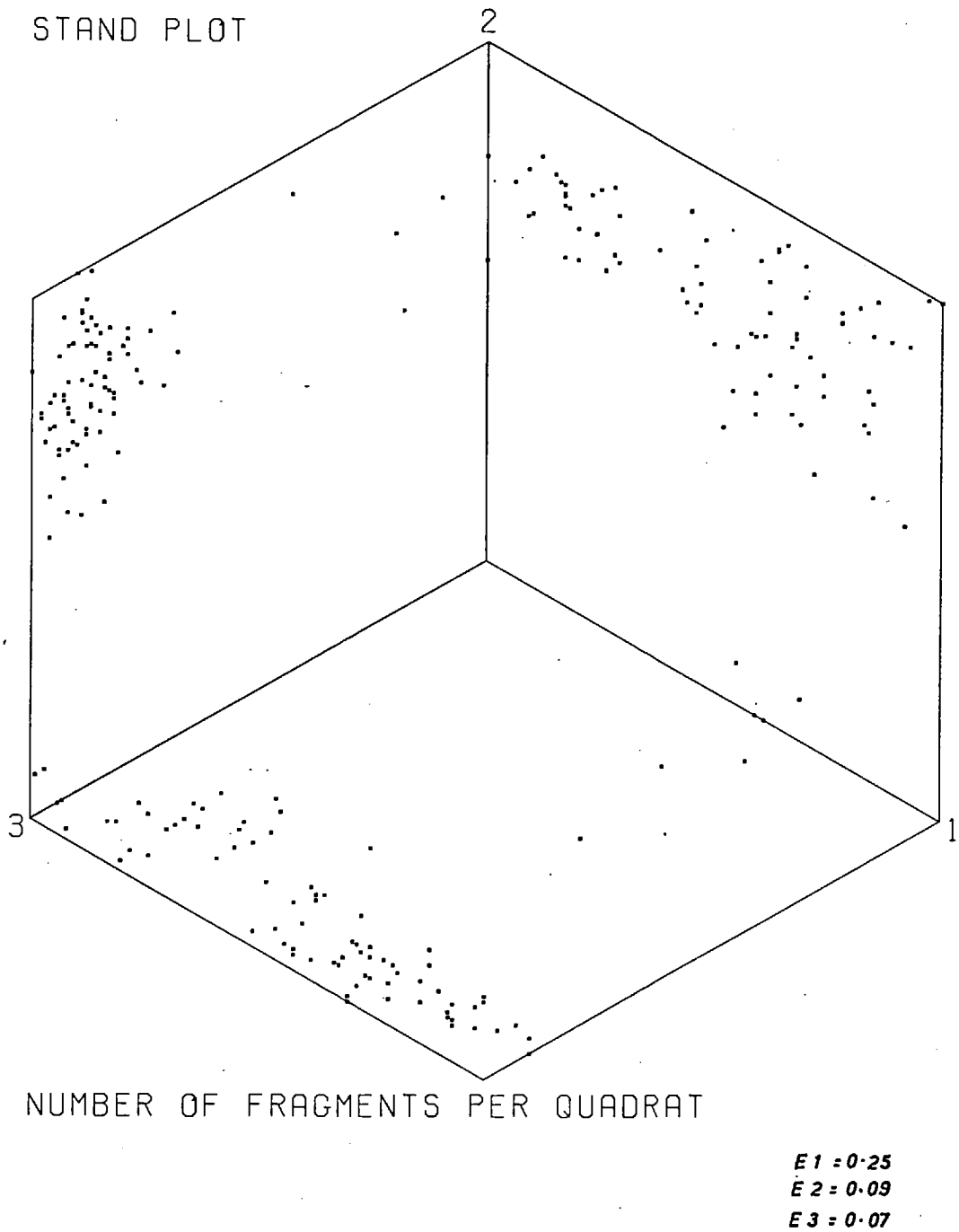


Fig. 58. Stand plot of fragment density based on data not including the densities of Nuphar, Typha and Acer.

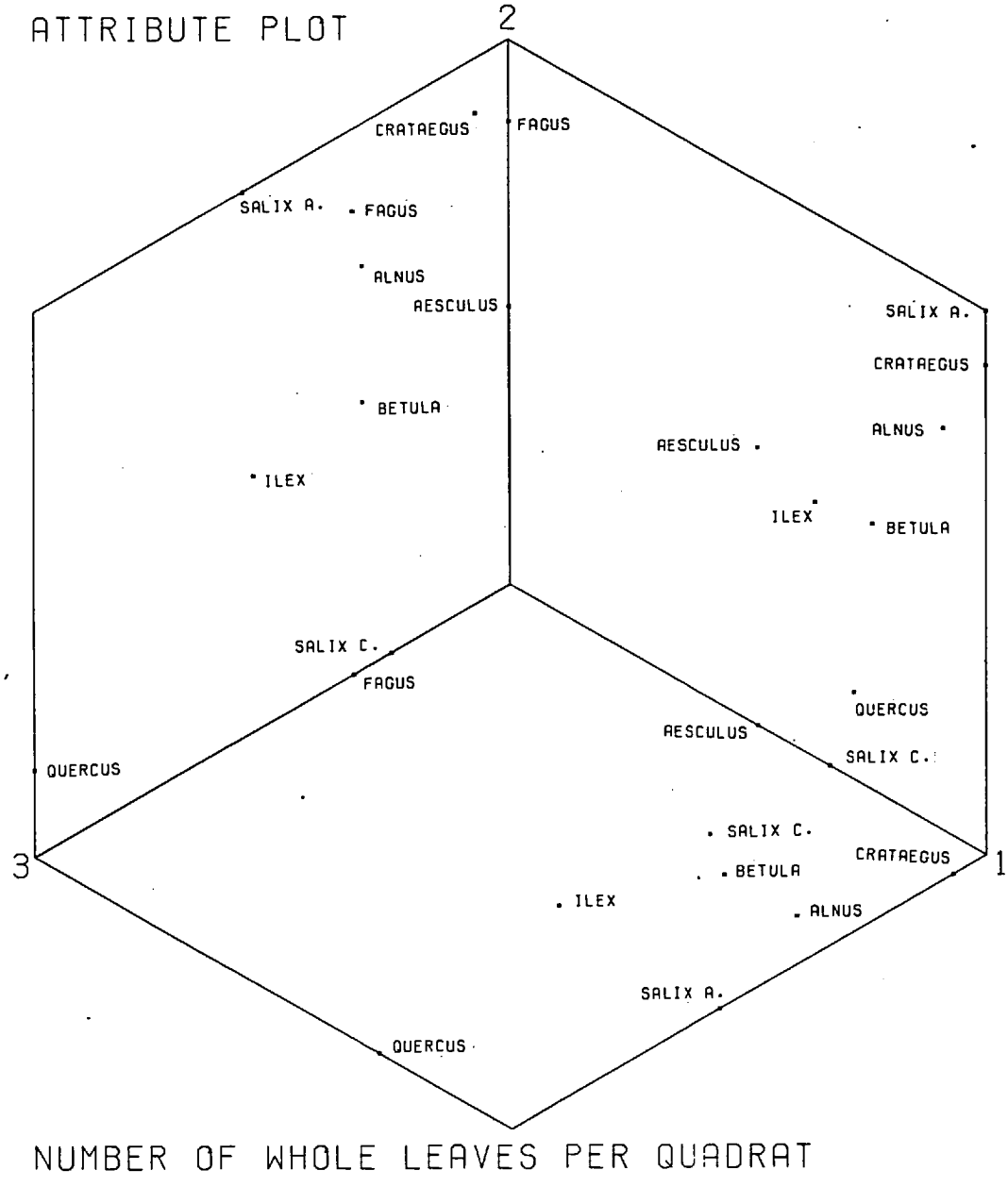


Fig. 59. Reciprocal Averaging species ordination plot based on the whole leaf density data from the surface sediment of Silwood delta.

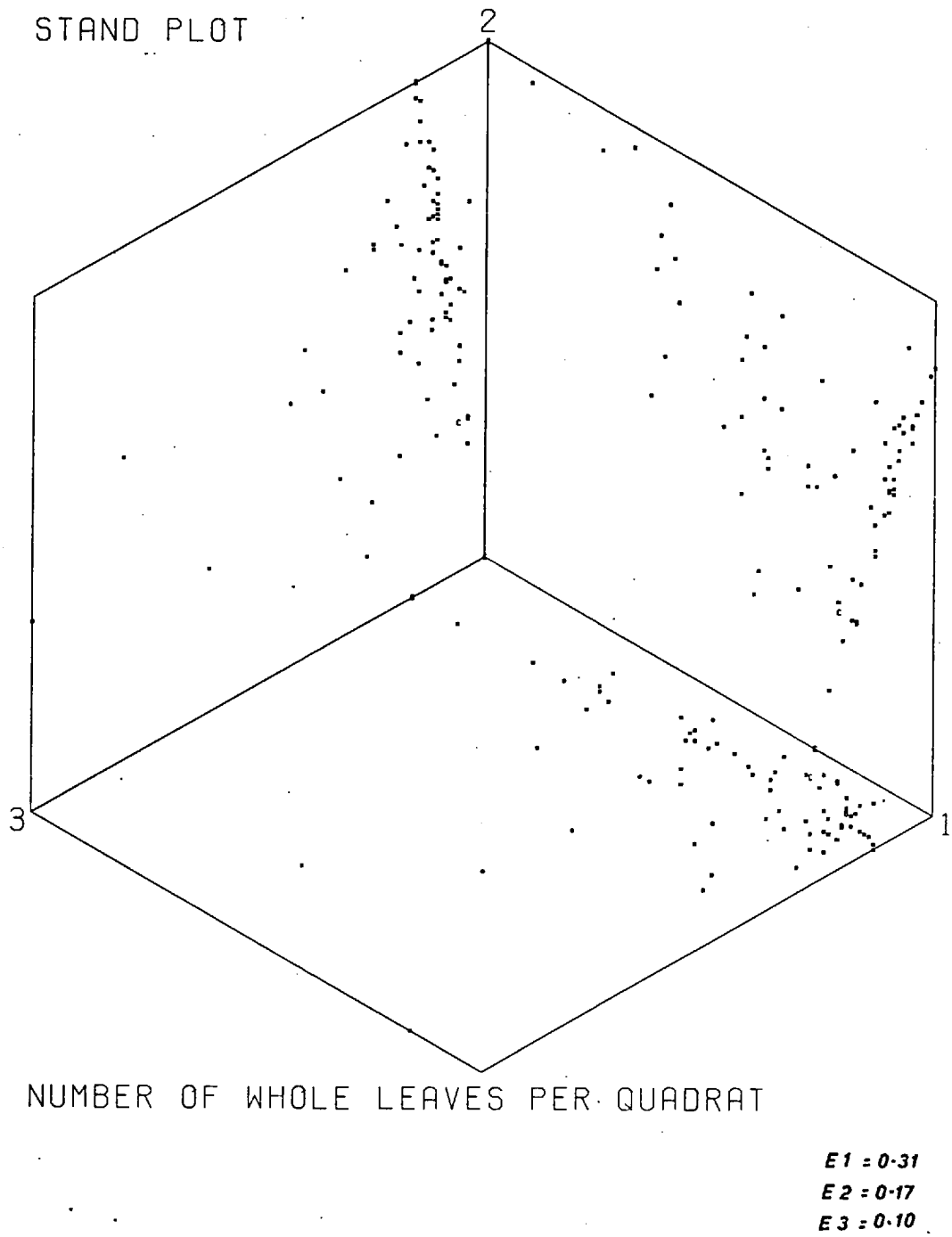


Fig. 60. Companion stand plot to Fig. 59.

preserved, even after the removal of Nuphar, Typha and Acer, suggesting that such a discontinuity is a strong characteristic of the data. The resultant separation of the stands into two groups facilitates mapping the delta surface in terms of species distributions. Fig. 63(a) shows the position on the delta of those stands occurring in the 'Fagus/Quercus' group. It is to be noted that they all occur around the stream distributaries 1 and 2 which, during the period of time sampling was carried out, carried an estimated 80% of the total stream flow (Fig. 8). Distributary 3, however, passed through the Typha bed before crossing the exposed delta surface, thus most of the leaves it may have been transporting were filtered out (McQueen, 1969). Distributary 4 was little more than seepage from the nearby bank.

It is, therefore, evident that the pattern of leaf fragment distribution on the delta surface is primarily controlled by the pattern and energies of the distributaries. Earlier it was pointed out that the majority of leaf fragmentation was the result of biological and mechanical degradation during water transport, thus it is not surprising that fragment pattern is associated with stream channel courses. It follows that any lateral species separation between the area of the distributaries and the rest of the delta surface must indicate spatial separation of species in the source vegetation. The Fagus/Quercus group revealed in Figs. 56 and 58 is clearly the result of stream transported fragments from the mixed woodland area upstream from Cascade bridge (Fig. 1). Whereas the remaining group of stands, comprising the 'Alnus group', represents the more local flora.

From the arguments presented in Chapter 10 the distribution of whole leaves on the other hand might be expected to reflect more strongly the effect of wind transport in determining dispersal patterns.

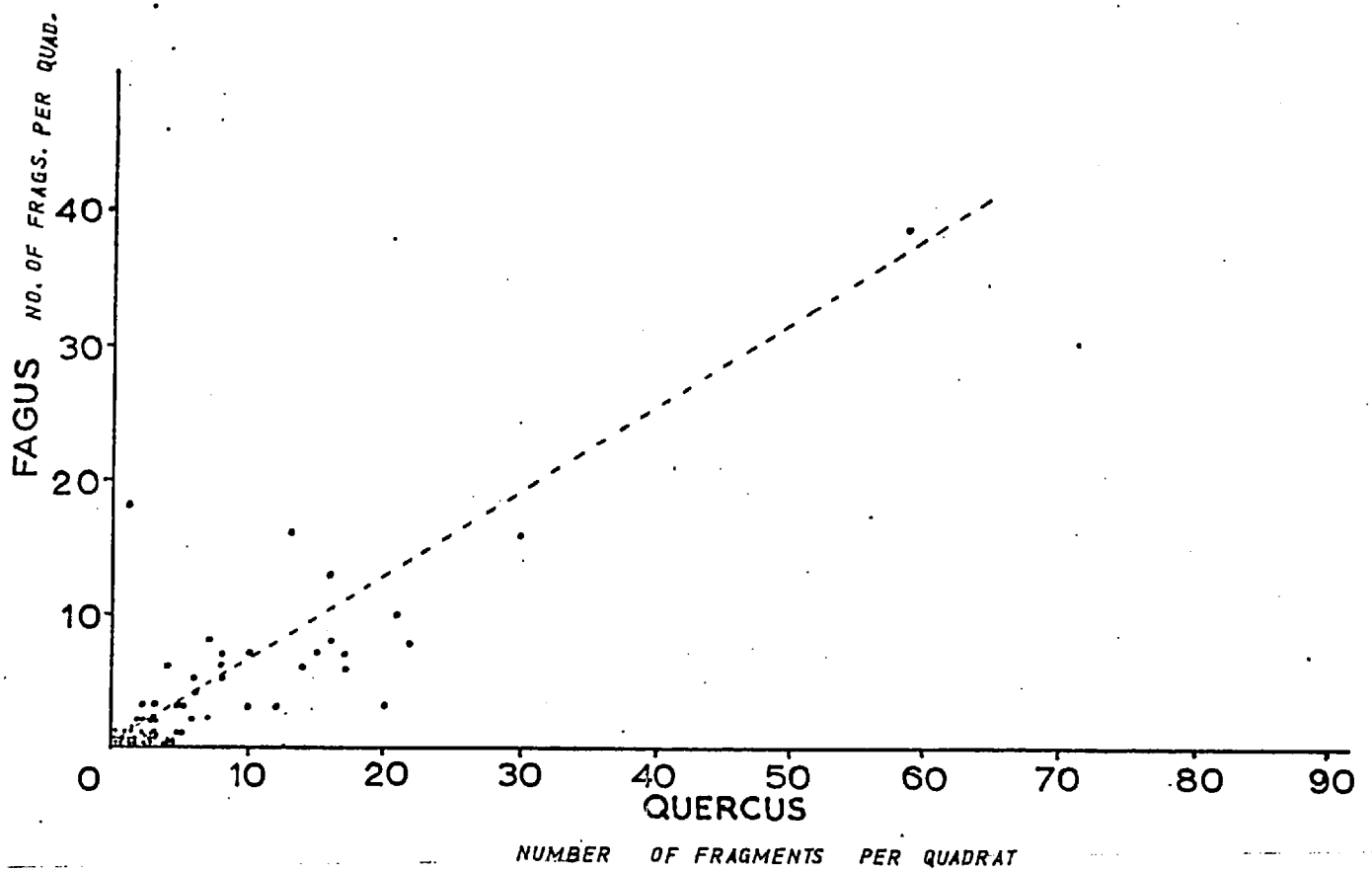


Fig. 61. The apparent relationship between the occurrences of Fagus and Quercus fragments indicated above was tested using Kendall's Rank Correlation procedure. It was found that the null hypothesis that the occurrences of the Fagus and Quercus were unrelated had to be rejected (See text).

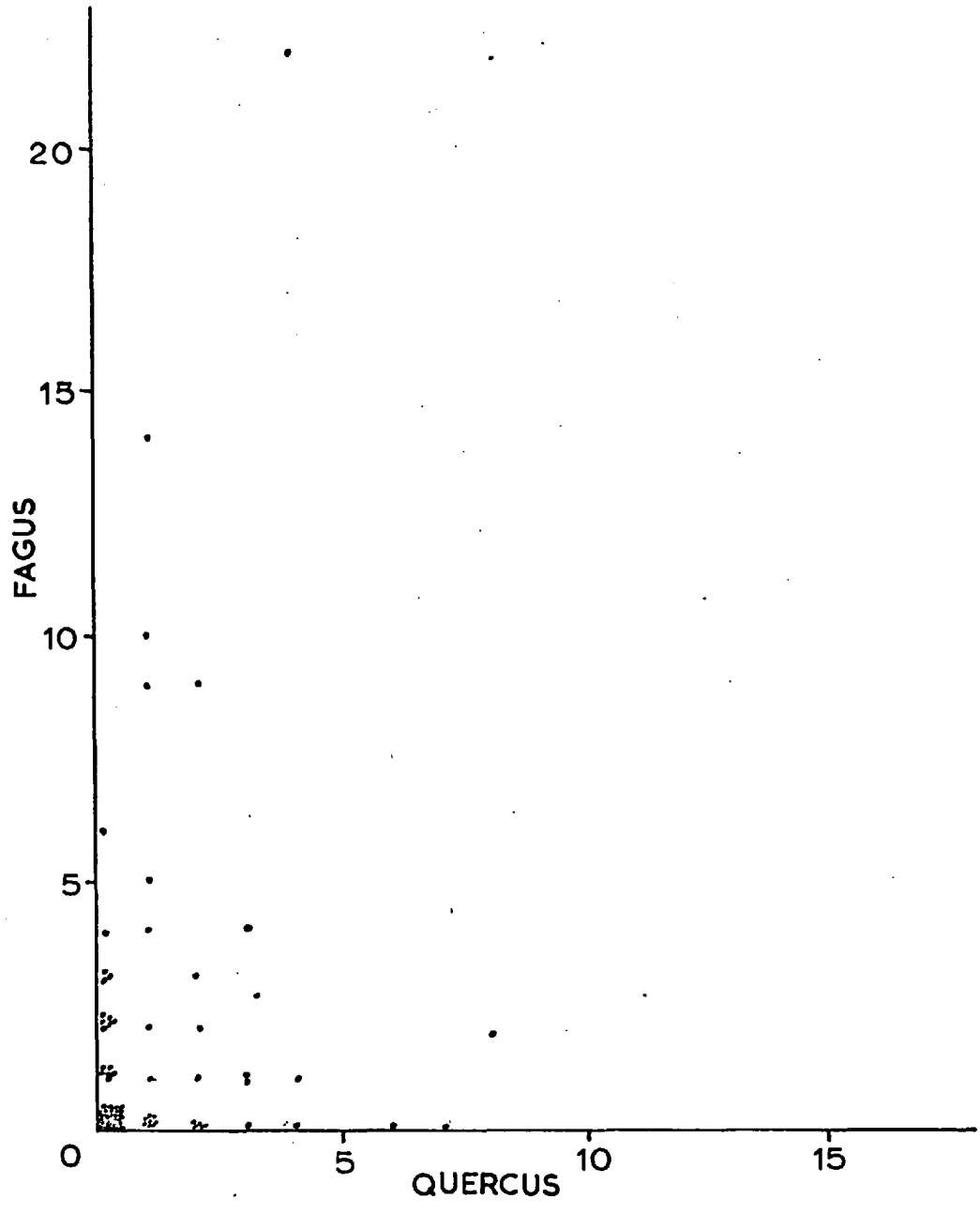


Fig. 62. The above diagram shows the numbers of whole leaves of Fagus plotted against the numbers of whole leaves of Quercus occurring in the same quadrat. It can be seen by inspection that there is no relationship between the occurrences of whole Fagus leaves and whole Quercus leaves in the upper sediments of the Silwood delta.

Figs. 59 and 60 show the results of an R.A. ordination of the whole leaf densities in the quadrats from the Silwood delta. The most striking feature about Fig. 59 is the separation, on axis 1, of Fagus, which suggests a marked difference in distribution from the other species. The stand plot, Fig. 60, shows no obvious discontinuities in the data, but there is possibly a gap halfway along axis 1. If stands with an axis 1 score less than 50 are plotted back on to the sample location map no clear pattern emerges, and certainly no pattern ascribable to stream channel effects. The diffuse nature of the Fagus group, if indeed it may be called a group, suggests that the variation in Fagus content between stands is high.

In the fragment density ordinations Fagus and Quercus plot close together which suggests that their distributions are similar. The whole leaf density distributions, however, are seen to be in no way related since Fagus and Quercus plot appart in Fig. 59. To demonstrate this more fully, Fig. 61 shows the number of fragments of Fagus plotted against the corresponding number of Quercus fragments occurring in the various quadrats. The significance of the apparent correlation between the numbers of fragments of Fagus and Quercus. occurring together in the Silwood delta quadrats, was tested using Kendall's Ranked Correlation procedure. This non-parametric test was adopted to ensure no false assumptions were made concerning the distributions of the two observations. Because of the large samples involved (n = 71) the value of S was obtained (S = 1113) and used to calculate

$$\frac{S\sqrt{18}}{\sqrt{[n(n-1)(2n+5)]}} = 5{\cdot}54$$

The significance was determined by treating this quantity as approximately a standardized normal deviate (Campbell, 1967). The

probability of obtaining such a large value when the two variables are unrelated is very small (less than 0.1%) therefore the conclusion is that the occurrences of Fagus and Quercus fragments are positively correlated. On the other hand, the whole leaf density distributions of the two taxa appear to be independent of each other (Fig. 62).

The delta water trap data (Table 2) show that approximately twice the number of Quercus leaves land directly on the delta surface by wind transport than Fagus leaves. On the other hand, from the results of the leaf degradation experiments (Figs. 28-43), it can be readily seen that Fagus is more resistant to both mechanical and biological degradation, resulting in a higher proportion of whole Fagus leaves surviving stream transport. This effect must have contributed to the large number of whole Fagus leaves recovered from the delta sediment quadrats: 175 as compared with only 69 whole Quercus leaves (Table 2).

From Fig. 59 it can be seen that on axis 1 Quercus plots close to the local species such as Alnus and Betula. The vegetation map (Fig. 2) shows that Quercus occurs in some abundance behind the Alnus trees bordering the lake and, in this respect, may also be regarded as local. Direct wind transport is the only way that leaves of these trees may enter the lake deposits, hence the Quercus plotting along with Alnus etc. on axis 1 of the whole leaf density ordination (Fig. 59). Axis 2, however, separates Quercus and Salix cinerea from the other species suggesting some differences in distribution; a difference that, in the case of Quercus, is more clearly shown by axis 3. The small numbers of whole Quercus leaves that do survive stream transport may account for this.

The position of Salix cinerea on the plots is worthy of some dis-

cussion. Although clearly a local species, the contribution of leaves directly to the delta by wind transport is small (Table 2). This is probably due to the fact that S. cinerea rarely attains a height in excess of 3 m on the delta and the Typha bed effectively traps any airborne leaves before they reach the lake. The majority of leaves must, therefore, enter the deposit via the stream and, as a result, S. cinerea consistently plots near to Quercus which exhibits a 'mixed' origin.

It is possible, therefore, to 'reconstruct' the Silwood vegetation, by examining the distribution patterns of fragments and whole leaves separately, as consisting of a local element, including such species as Alnus, Betula and Salix alba, and an extra local element rich in Fagus. Quercus appears to be a component of both local and extra local floras, as apparently is Salix cinerea. The position of Ilex, Aesculus and Crataegus appear to be intermediate.

The special position of Nuphar may at first present some problems but anatomical studies would so soon reveal its aquatic habit. Thus some measure of palaecommunity reconstruction may be possible using only density measures of fragments and whole leaves.

Cover abundance measures

If the area of each individual fragment is measured, and it is assumed that the majority of leaves are lying parallel to the bedding planes, the total area per quadrat of that species may be considered comparable to a fragment cover estimate. (There is no point in calculating the percentage cover since all the quadrat volumes are the same.)

Fig. 64 presents a plot of the total fragment areas per quadrat

of all the leaves of the twelve taxa found in the Silwood delta sediments. Axis 1 clearly separates out Nuphar from the other species (e.g. Fig. 55) and reference to the raw data (appendix table 3) suggests a possible reason. Apart from the difference in distribution, the morphology of the large Nuphar pads is totally different from any of the other species, consequently fragments can exhibit a much greater size range than any other species. The total area of Nuphar can therefore be seen to fluctuate greatly from quadrat to quadrat. The data concerning Aesculus, which also has comparatively large leaflets, also shows this pattern which is again reflected in the ordination of Fig. 64 since Aesculus is separated from the other species on both axes 2 and 3.

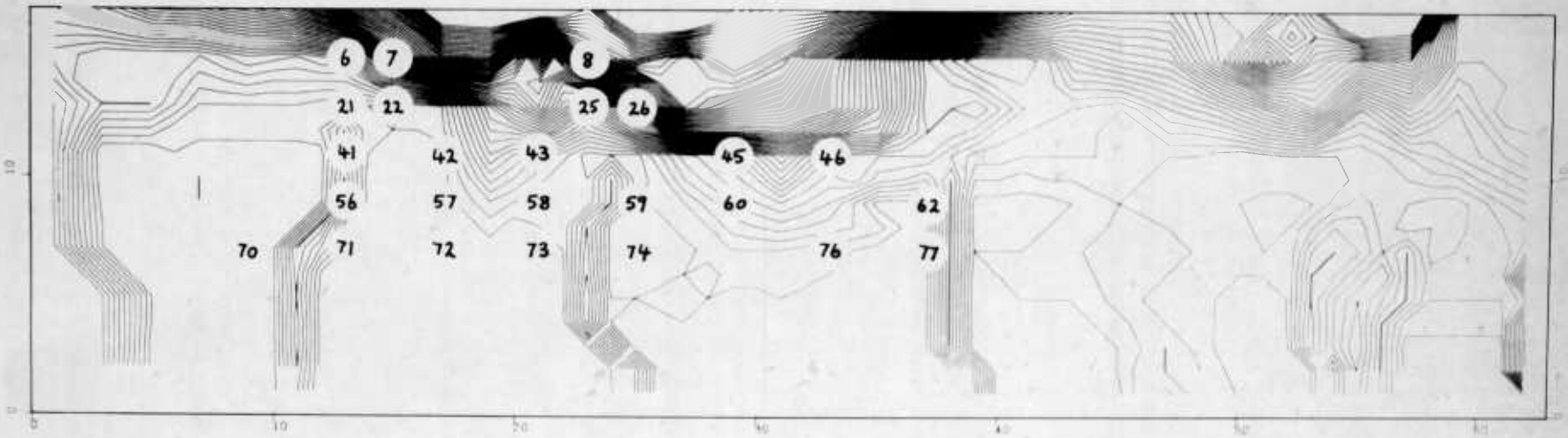
The stand plot (Fig. 65) reveals an apparent break in the ordination along axis 2; the lower group coinciding with the positions of the taxa Salix cinerea, Crataegus, Ilex, Quercus, Fagus and Acer on Fig. 64. The position of these stands on the delta surface is shown in Fig. 63(b). Clearly the pattern derived from the density measures (Figs. 55 and 56) is being repeated, which suggests that the abundance measures in this instance, in spite of the powerful morphological effect, are retaining sedimentary pattern information.

The ordination would not, however, be so easily interpreted if one of the species determing the lower group was morphologically very different from the others. This effect can be seen to some extent in Figs. 66 and 67. Here the species not occurring as whole leaves (Nuphar, Typha and Acer) have been excluded. The morphological effect, linked with the occurrence of Aesculus, now dominates the ordination resulting in this species plotting away from the others. As Aesculus was, to some extent, contributing towards the separation of the Fagus/Quercus group on axis 2 of Fig. 65, the separation of the

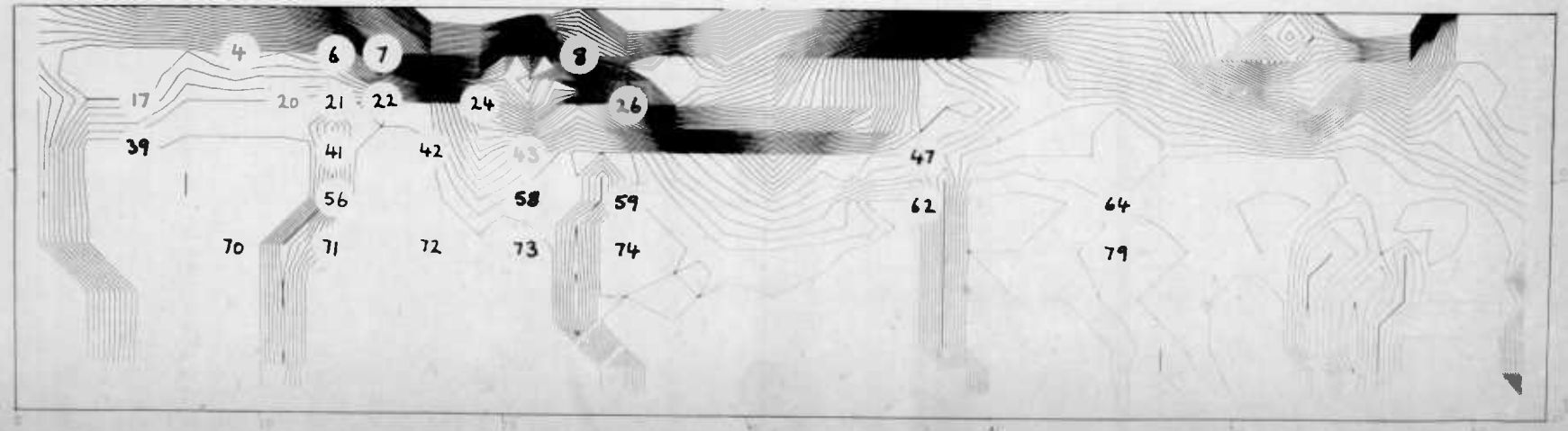
Fig. 63(a). The diagram opposite shows the positions of those stands comprising the '*Fagus*/*Quercus*' group of Figs. 56 and 58 with respect to the delta contours. The ordination was carried out using density data.

Fig. 63(b). The positions of the stands occurring in the lower group on axis 2 of Fig. 65. This group, again rich in *Fagus* and *Quercus*, is the result of an ordination based on 'cover' data.

(a)


6
7
8
21
22
25
26
41
42
43
45
46
56
57
58
59
60
62
70
71
72
73
74
76
77

(b)


4
6
7
8
17
20
21
22
24
26
39
41
42
43
47
56
58
59
62
64
70
71
72
73
74
79

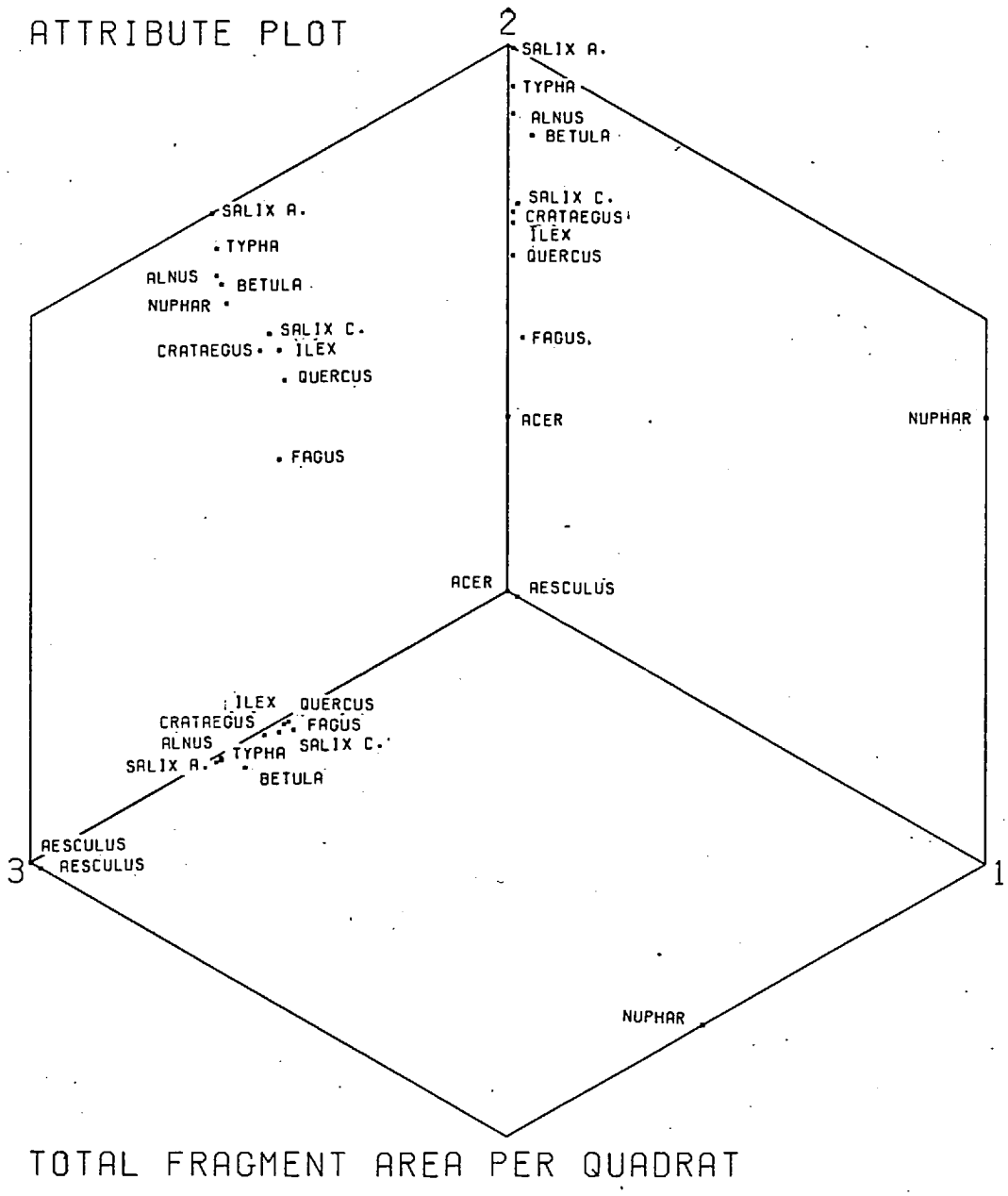


Fig. 64. Reciprocal Averaging ordination of leaf fragments from the Silwood Delta surface sediment based on 'cover' rather than density.

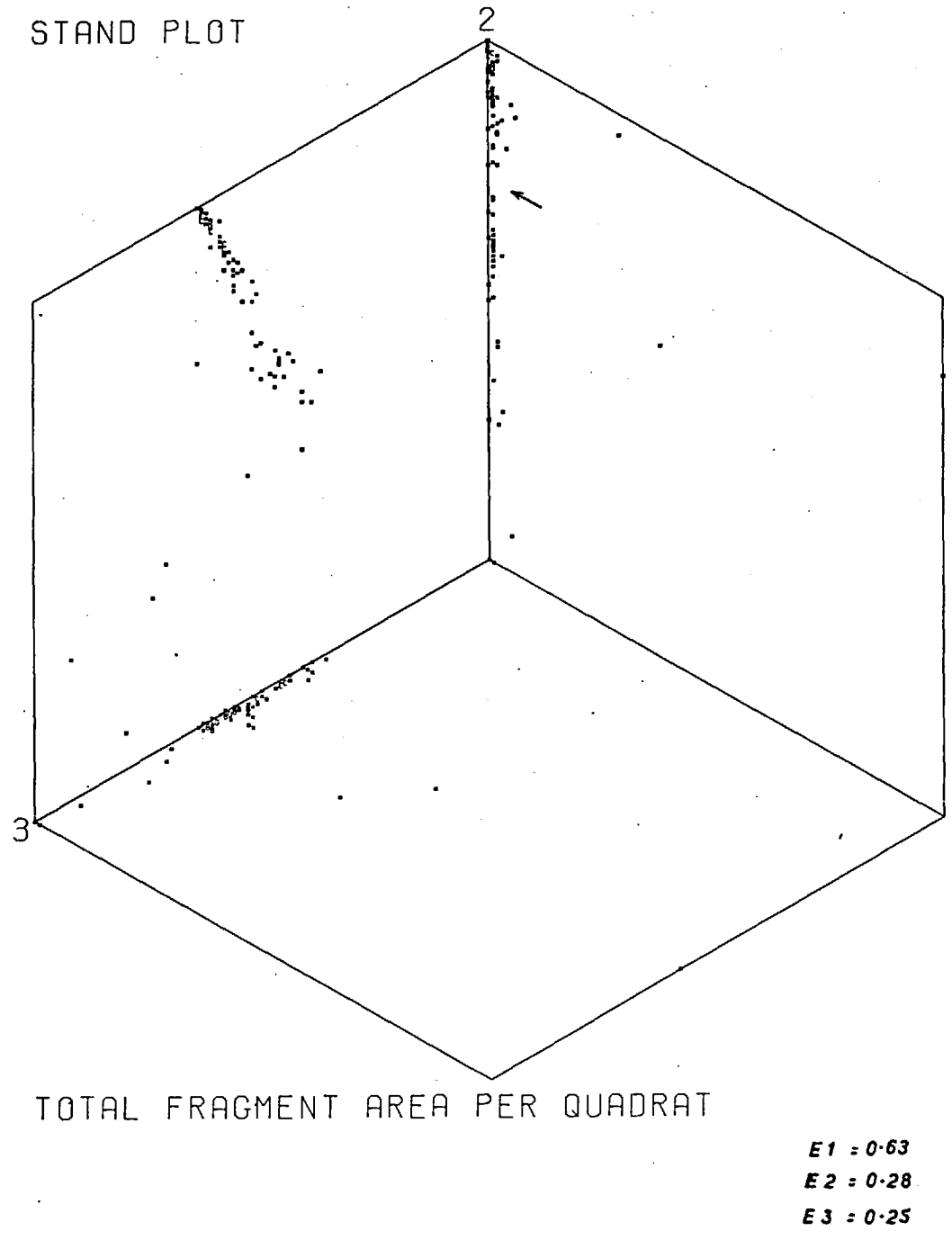


Fig. 65. An apparent discontinuity in the stand ordination on axis 2 is arrowed. Those points below the arrow represent those stands relatively rich in Fagus and associated species.

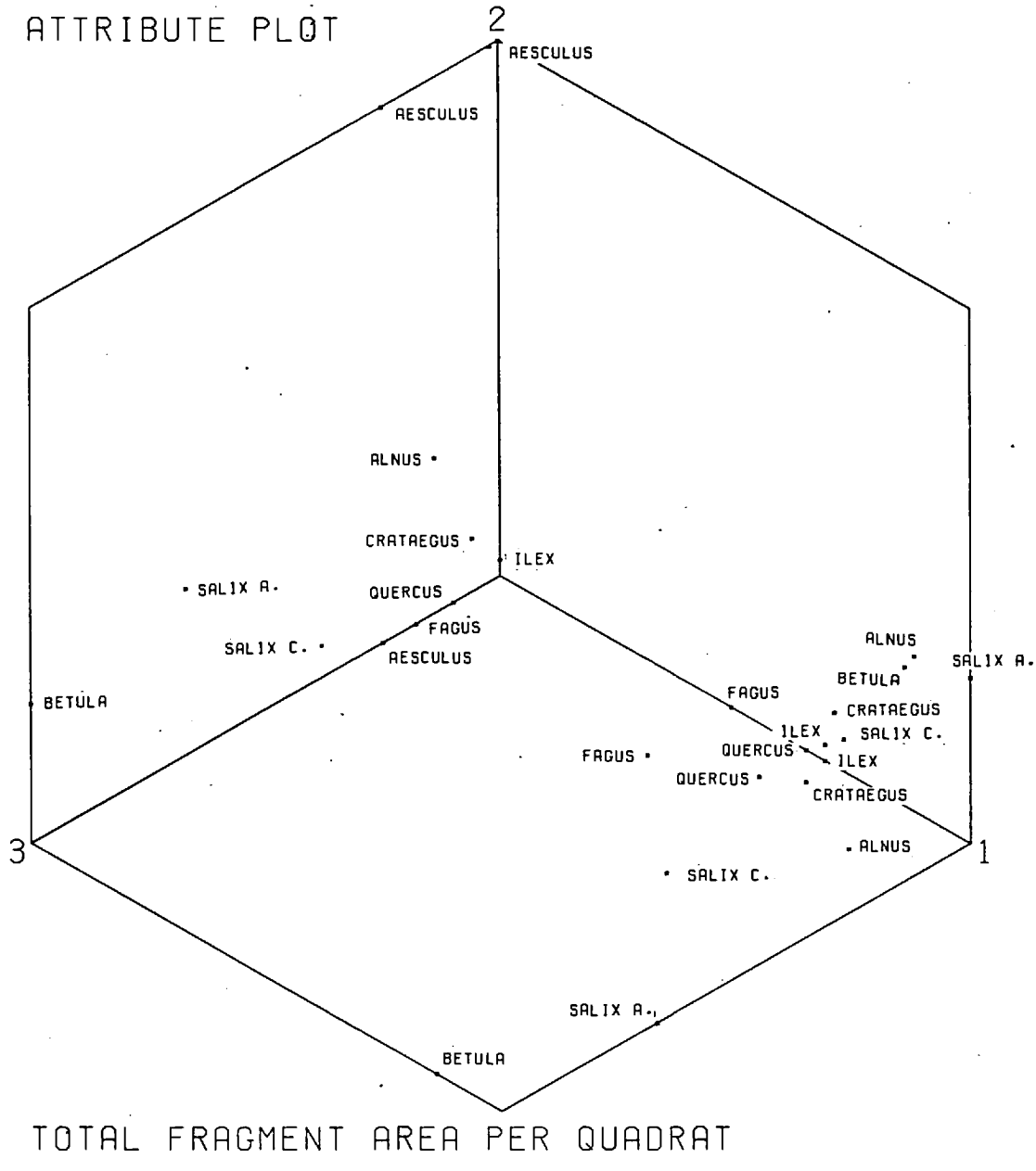


Fig. 66. Reciprocal Averaging ordination based on 'cover' abundance of 9 taxa: Fagus, Quercus, Alnus, Betula, Salix cinerea, Ilex, Aesculus, Salix alba and Crataegus.

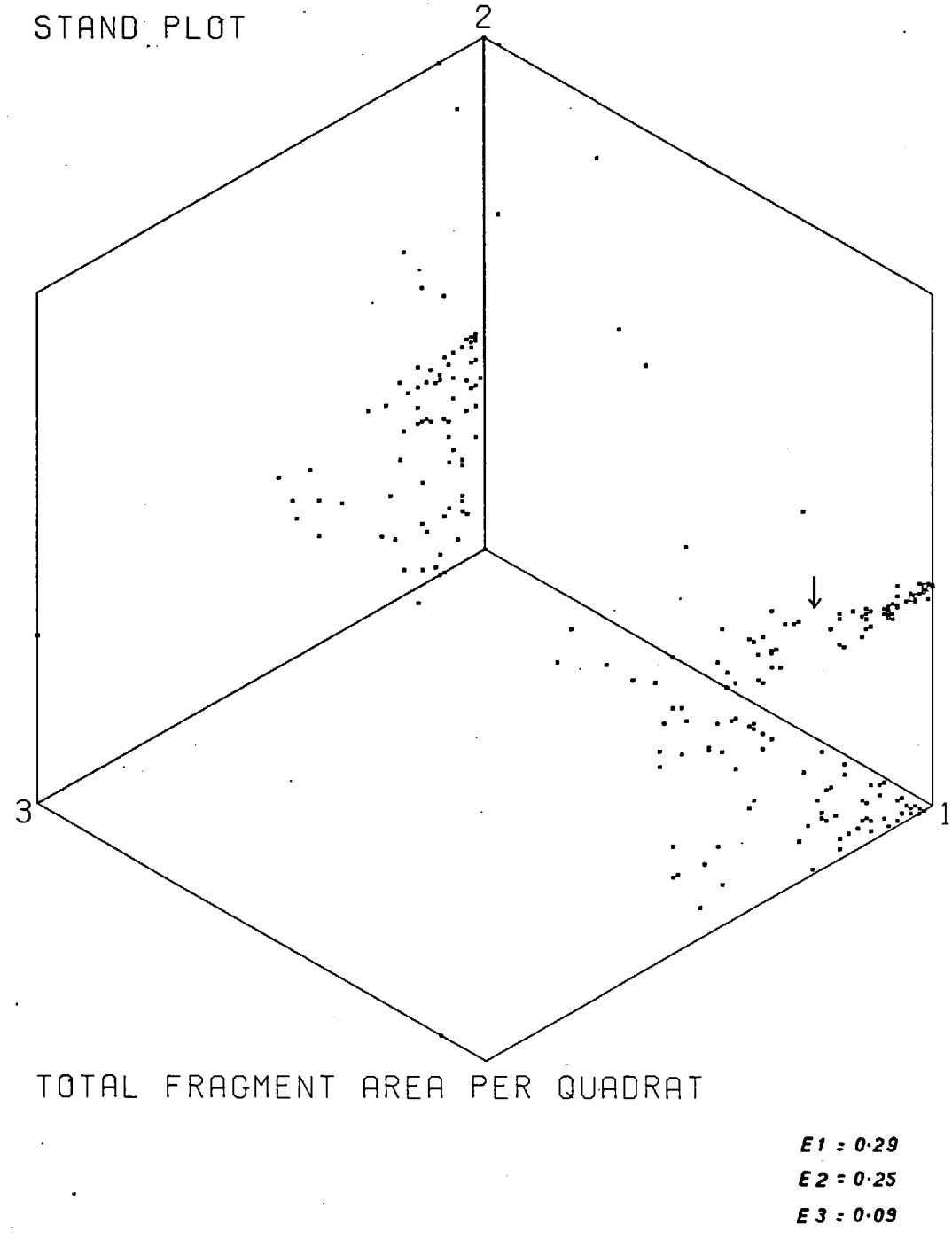


Fig. 67. A stand ordination based on 'cover' abundance and a companion plot to Fig. 66. An apparent discontinuity of the ordination on axis 1 is arrowed.

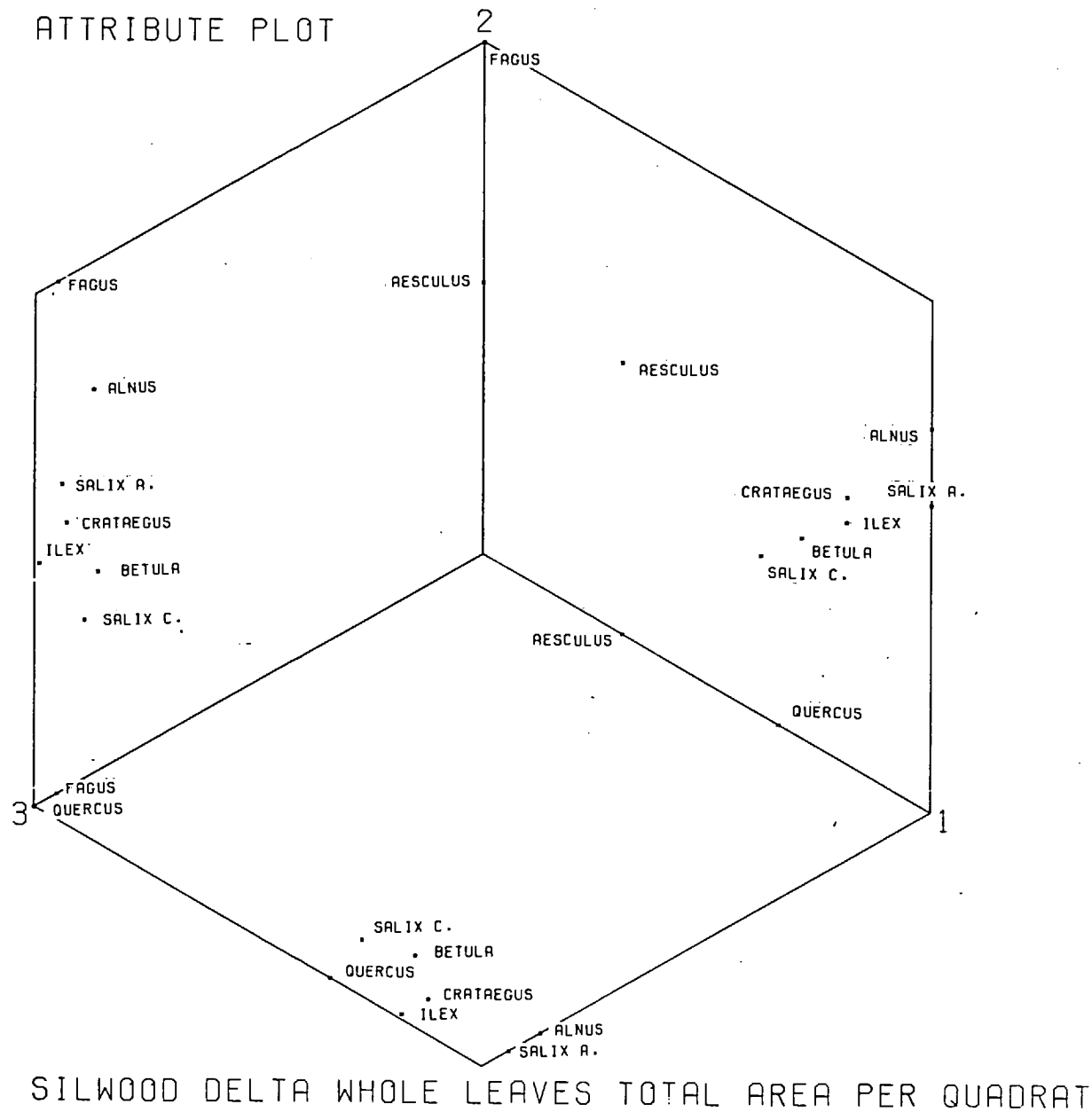


Fig. 68. A species plot of 'cover' data of whole leaves only.

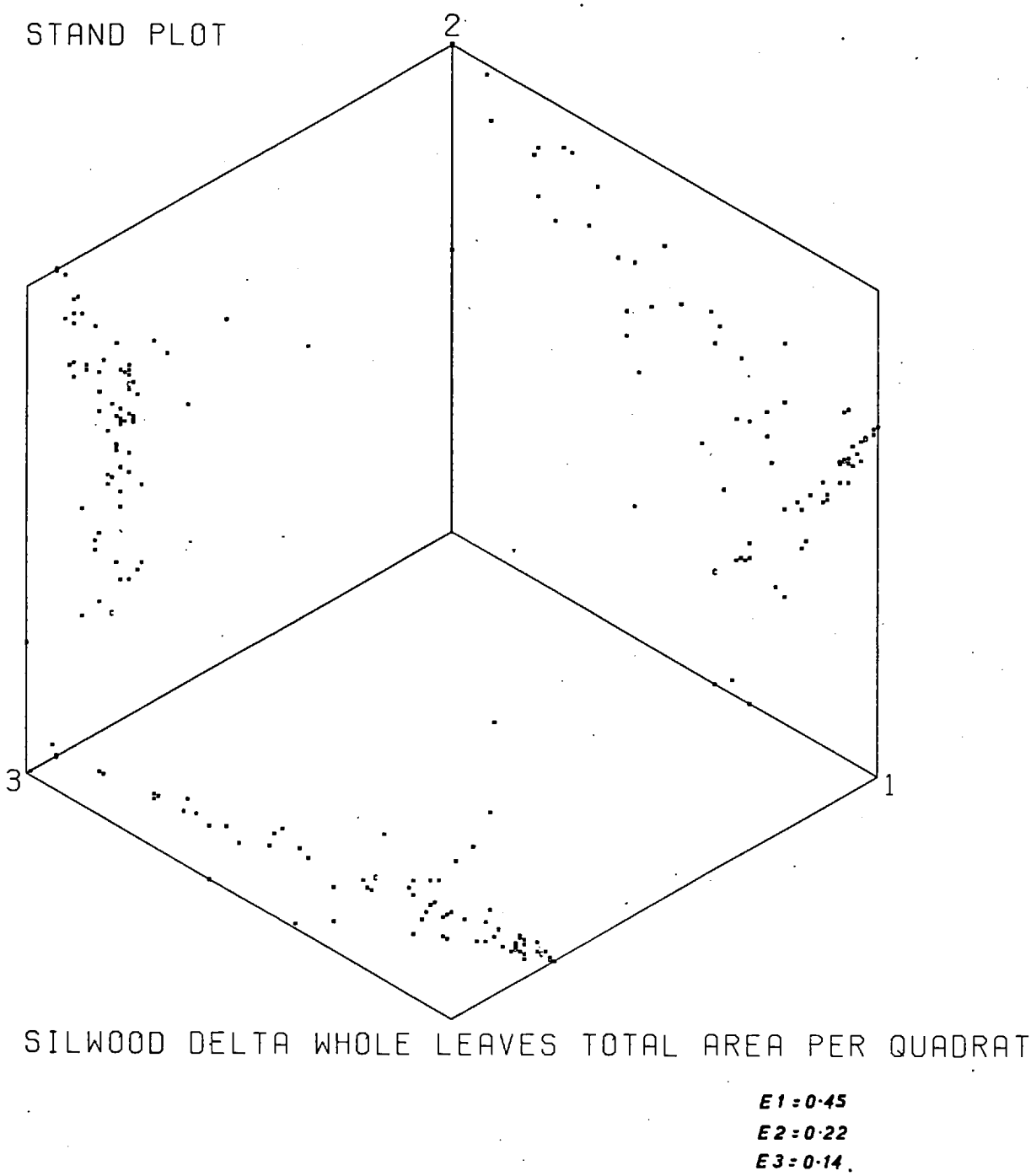


Fig. 69. The companion stand plot to Fig. 68.

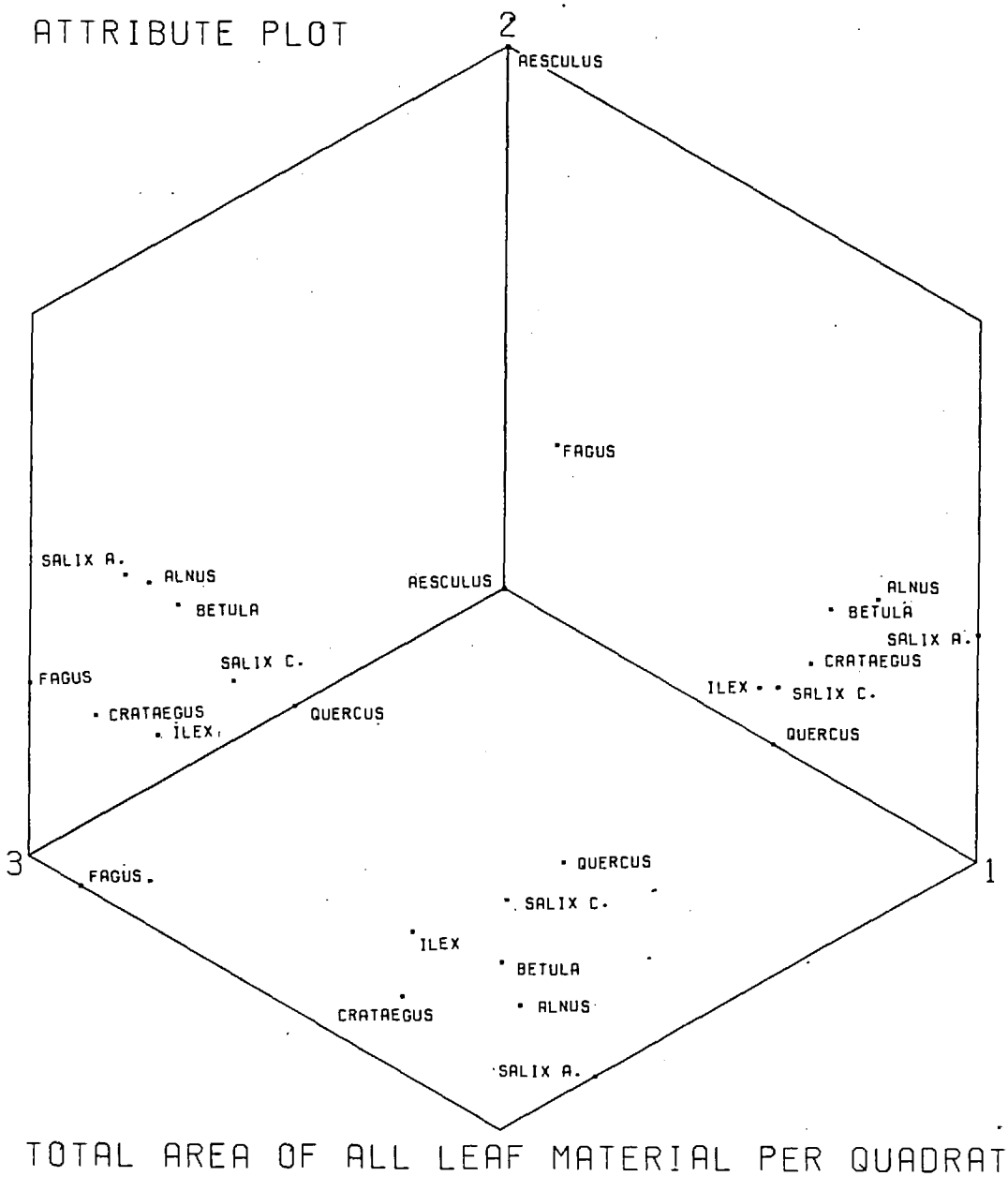


Fig. 70. A Reciprocal Averaging ordination of the combined whole leaf and fragment 'cover' abundances data.

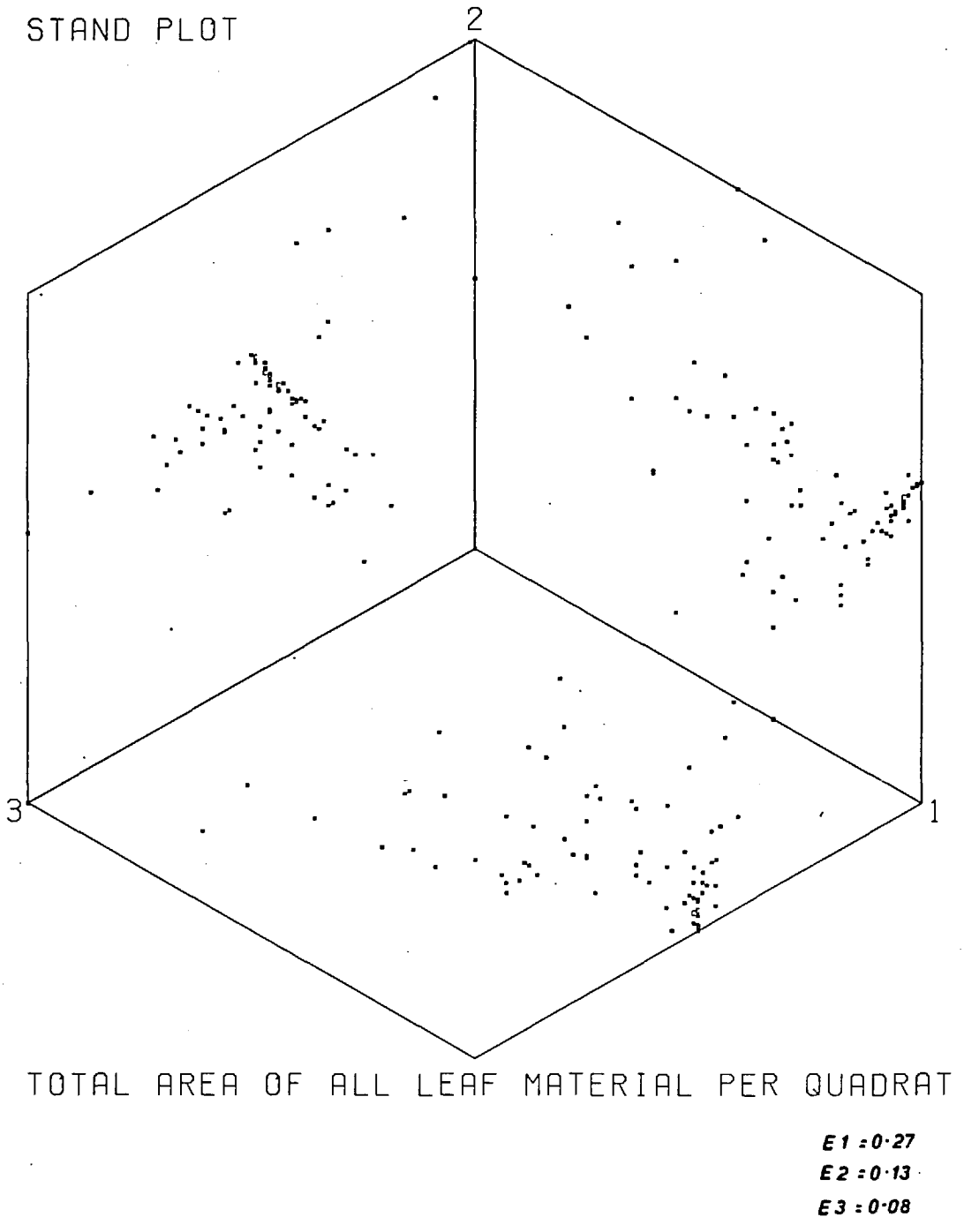


Fig. 71. The companion stand plot to Fig. 70.

stands into two groups is not so well defined. However, those stands occurring to the left of the arrow on axis 1 (Fig. 67) are, in fact, the same as those plotted in Fig. 63(b).

When the species are ordinated on the basis of the whole leaf total area per quadrat (Fig. 68) Fagus is separated from the other species on axis 1 as it was when ordinating the whole leaf density data (Fig. 59). However, Aesculus is separated further from the main group and its difference picked out strongly on axis 3. Once again, this may be interpreted as primarily a morphological effect. Other than this, the distribution of the species on axes 1 and 2 is very similar to that resulting from the density data. Similarly, the stand plot (Fig. 69) exhibits the same pattern, on axes 1 and 2, as in Fig. 66. The variation on axis 3, however, now separates those stands rich in Aesculus rather than Quercus. Thus the separation of Quercus from the 'local' group, due to its mixed origin, now becomes overridden by the powerful morphological influence associated with Aesculus.

If the whole leaf and fragment areas are combined to give the total area for each species per quadrat the resultant ordination has the appearance of Figs. 70 and 71. This type of data approximates to a cover abundance measure for each species.

The magnitude of the data scores for species which are local to the site, and those with leaves resistant to degradation, will tend to be largely determined by the number and size of the whole leaves. For the others fragment size and number will be important. Clearly those taxa producing large leaves will amass large cover scores even if only a few individuals are present in each quadrat. As expected, therefore, the morphological influence on the ordinations is very

strong with the result that Aesculus plots away from the main group on all three axes. Fagus, however, is also separated on both axes 1 and 2. The reason for this is probably not so much morphological as resistance to degradation. By reference to Table 3 it will be seen that Fagus fragments only comprise some 26% of the total area of Fagus occurring in the sampled delta deposits. Thus where Fagus occurs the cover will often be determined by the number of whole leaves. Table 2 shows that the contribution of whole leaves to the delta by direct aerial transport will not add significantly to the total Fagus cover score. Therefore, whole leaves transported by the stream will largely determine the total Fagus area per quadrat, but, unfortunately, the high cover scores of the local species swamp the stream controlled Fagus pattern. Under conditions where all stream transported taxa are easily degraded the situation would become even worse, and any pattern caused by sedimentary processes would be lost. The prospects of detecting such patterns would, however, be much better if density measures were used since, with increased degradation, the fragment density in the distributories would be increased, hence a better 'contrast' between the stream distributories and the rest of the delta surface would be obtained.

THE THREE DIMENSIONAL STRUCTURE OF THE SILWOOD DELTA

In order to determine the three dimensional structure of the Silwood delta, 7.5 cm diameter cores were taken at the positions shown in Fig. 11 by the method described in chapter 7 . Diagrams of the cores so obtained are shown in Figs. 72-76.

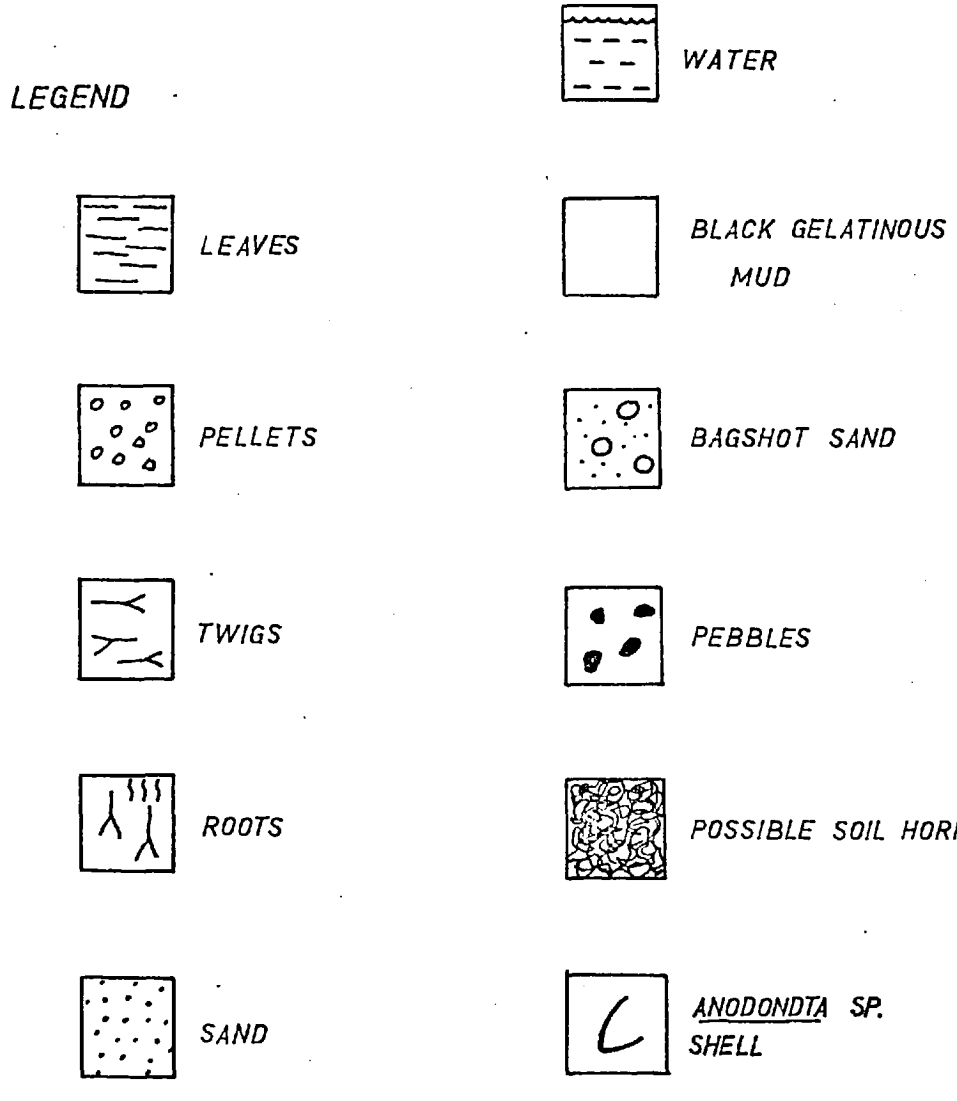
The plant remains

With one exception, the uppermost portion of all cores, although semi liquid, exhibited pronounced concentrations of leaf material (leaf bed 1) and in some cases these were admixed with small quantities of coarse silt. Although of variable thickness, leaf bed 1 never extended more than 0.2 m below the sediment surface. The core taken in 0.45 m of water lacked a concentration of leaf material at the top of the core, indicating that at this water depth on the delta slope leaf deposition was minimal. Below 0.2 m the occurrence of leaves in the cores became rare until, at 0.7-0.8 m another concentration of leaves (leaf bed 2) was encountered. Leaf bed 2 was some 0.2 m thick and interspersed with pellets of inorganic sediment. These pellets, although widespread laterally, only occurred at this depth (see sediment description).

In many cores were found rootlets in growth positions associated with, and below, leaf bed 2. The presence of these roots often extended down to a dense layer of well preserved leaves overlying, in some instances, a layer of sand. Although leaves were usually not common in the sand layer itself, twigs and Fagus cupules were sometimes found. Immediately below the sand layer there occurred yet another concentration of leaves, but somewhat poorly preserved compared to those overlying the sand. Below this leaf bed, leaf remains became rare and the

Figs. 72-76a Diagrams of cores taken from the delta in the positions shown in Fig. 11. On the left of each figure the depths in metres below the sediment surface are shown.

Fig. 76b Diagram of a hypothetical core summarizing the structure of the delta.



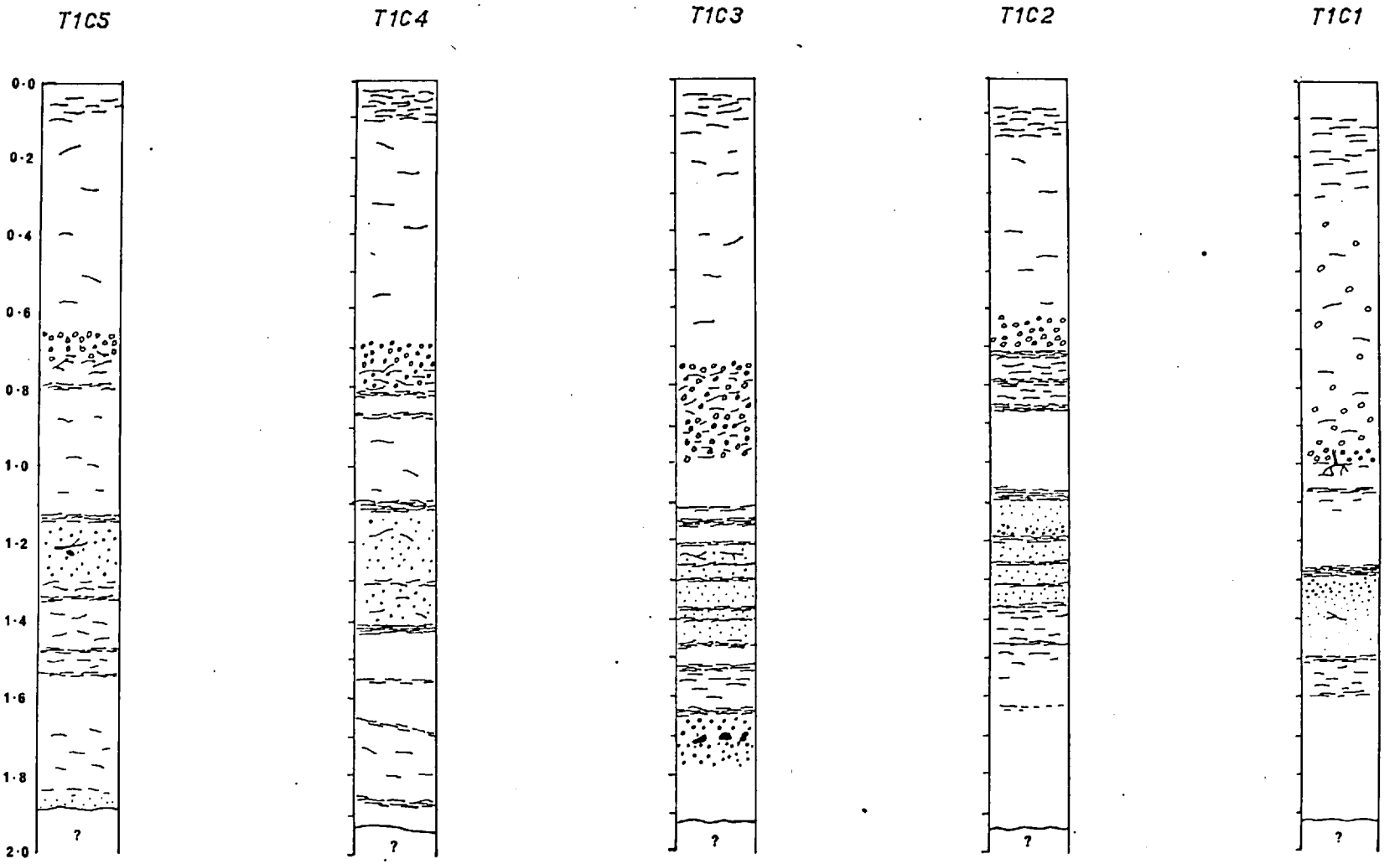


Fig. 72

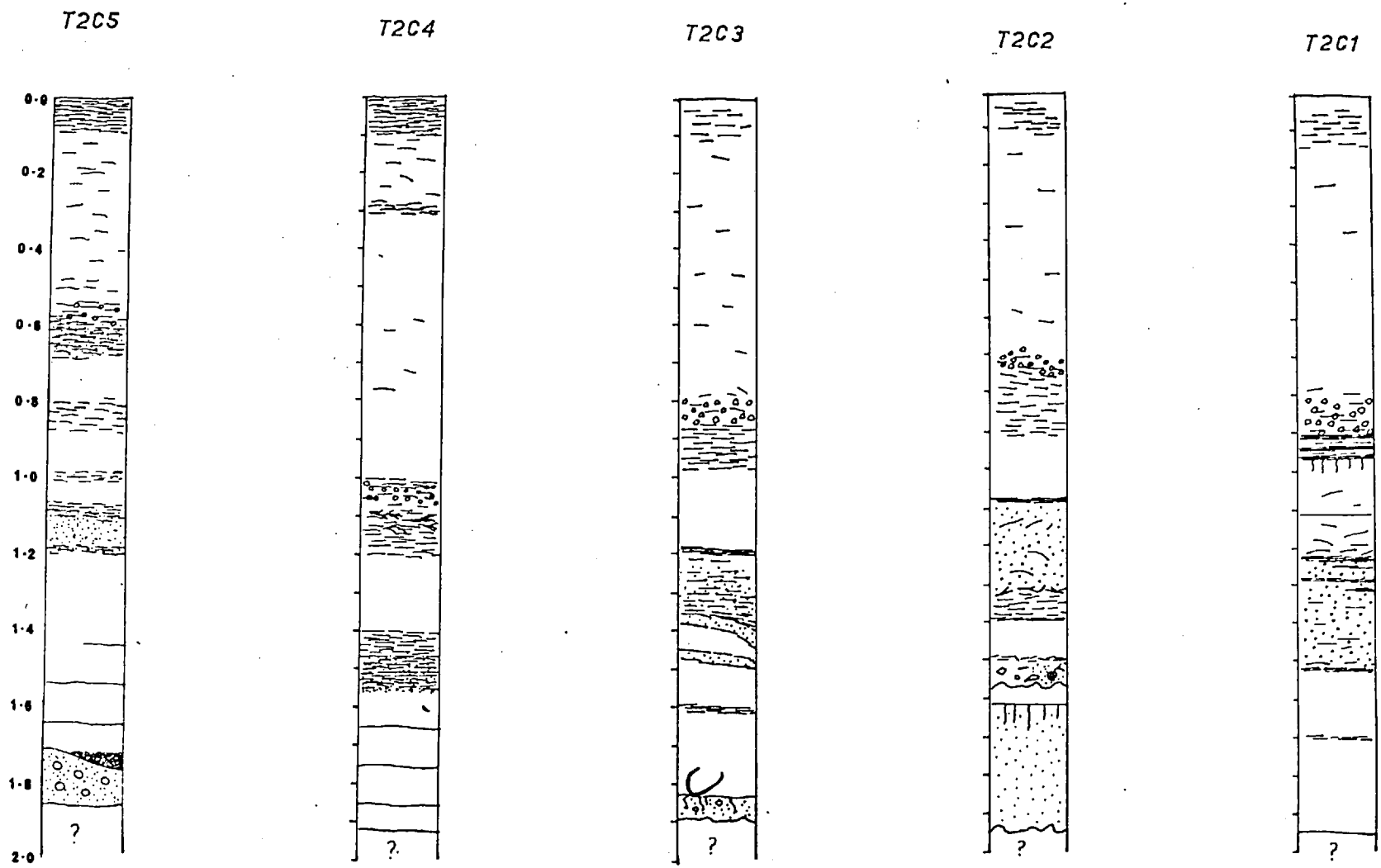


Fig. 73

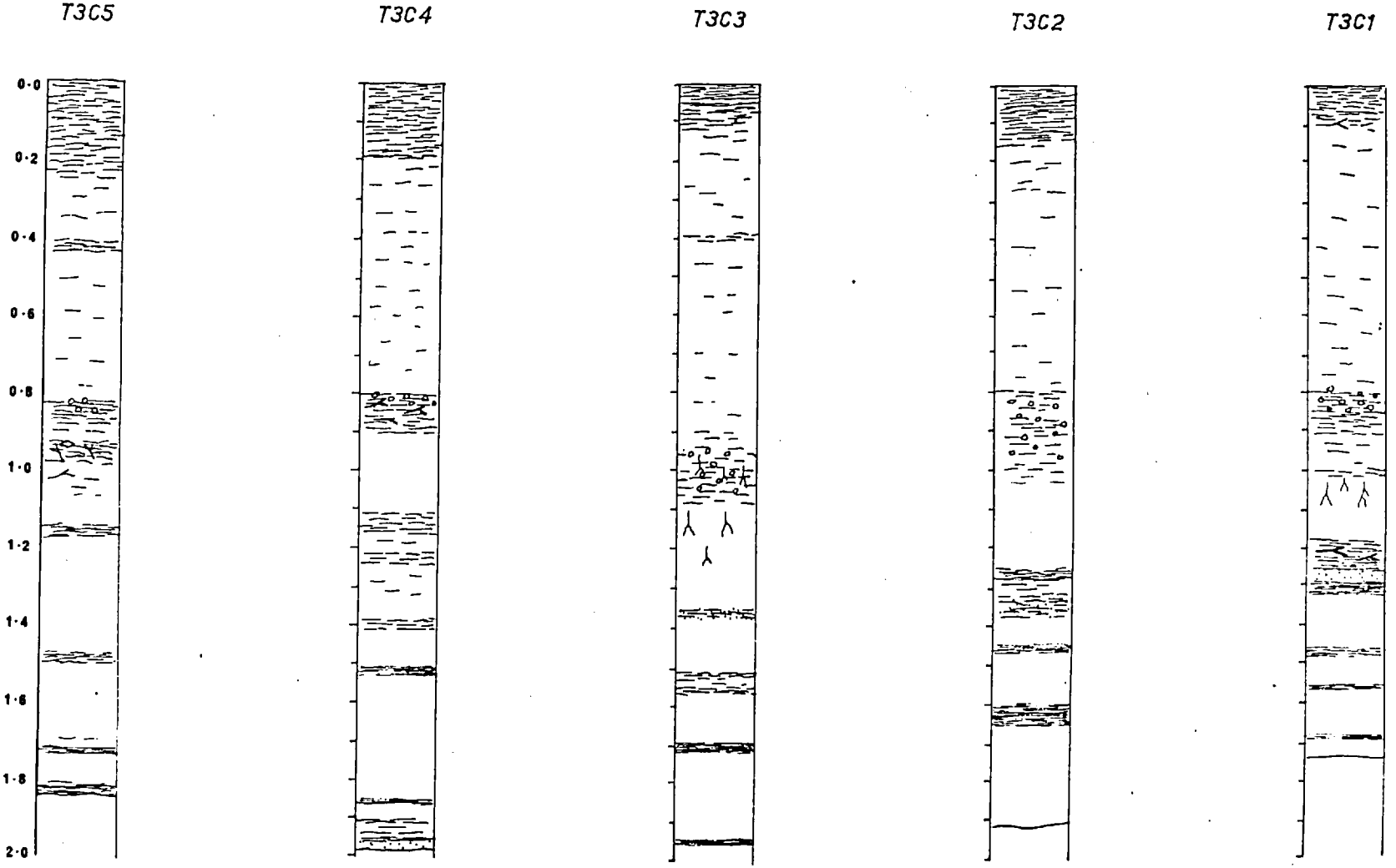


Fig. 74

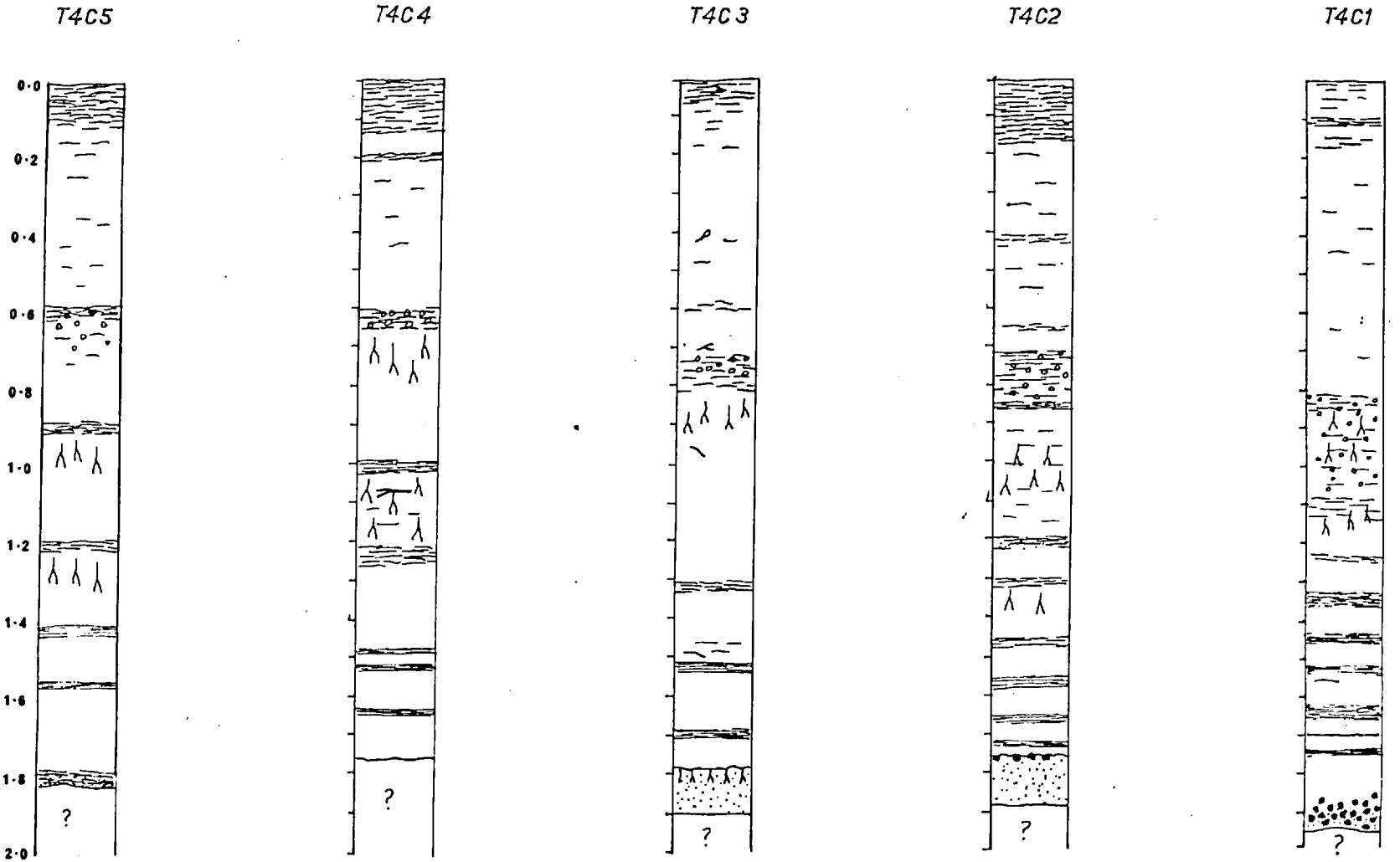


Fig. 75

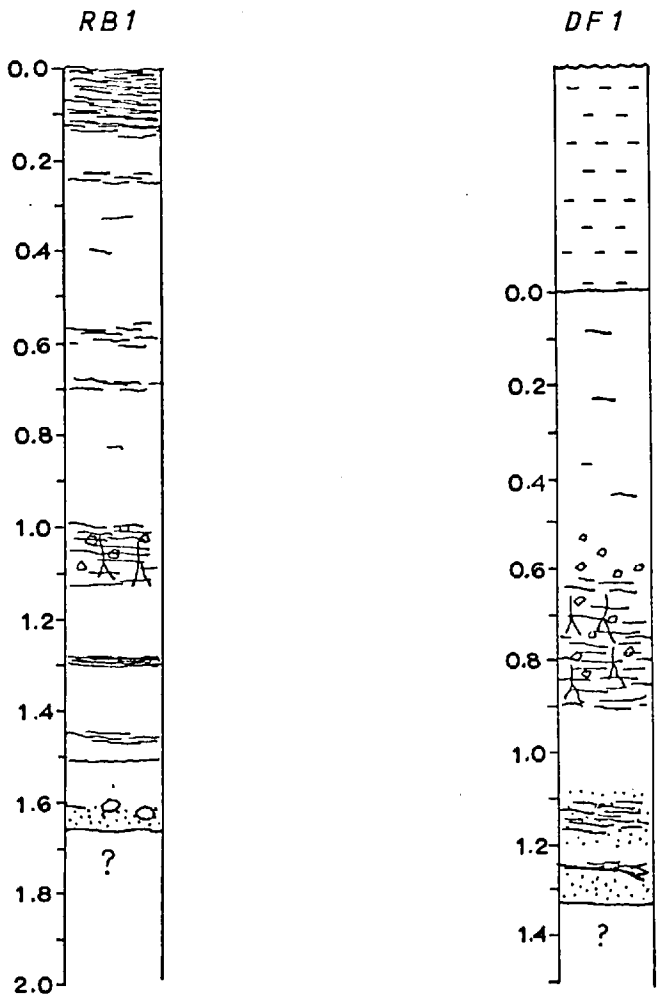


Fig 76(a)

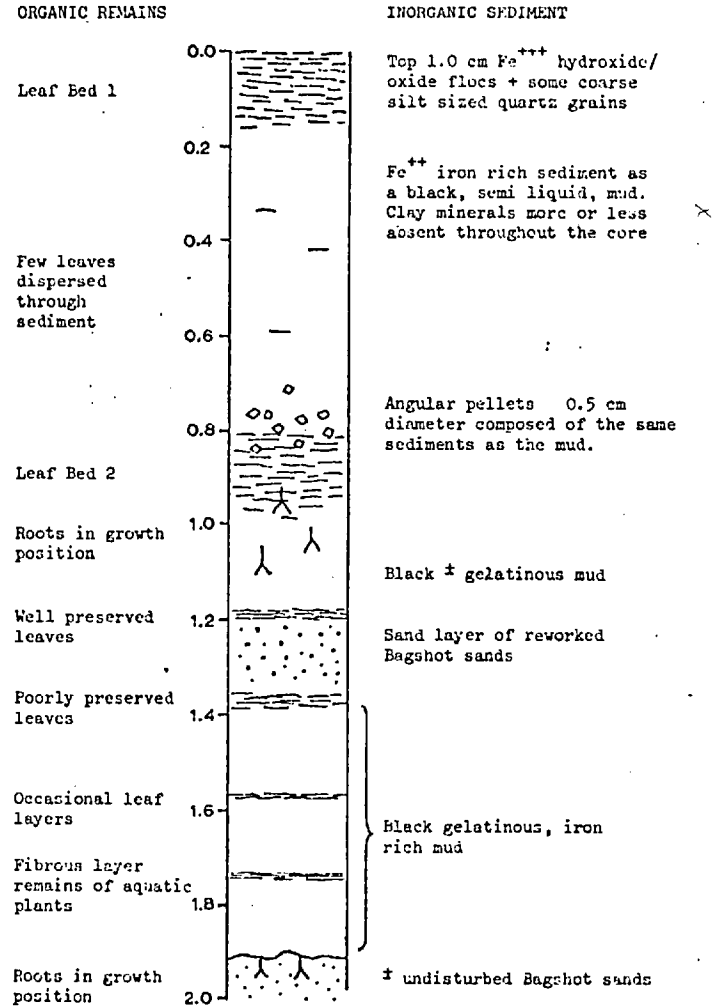


Fig 76 (b)

only evidence of macro plant remains was in the form of layers (not more than 0.1 m thick) of fibrous material which may represent the remains of an unidentified aquatic plant.

It was not possible to quantitatively analyse the species distribution of leaves between the cores. However, subjective analysis of leaf remains washed from the sediment showed that the species composition of leaf beds 1 and 2 was very similar: both were rich in Fagus and Quercus leaves, with some Ilex cuticles.

The inorganic sediment

The uppermost centimetre or so of sediment on the delta was orange brown in colour and consisted of flocculent ferric hydroxide admixed with a small silt sized quartz fraction. However, much of the silica of this surface sediment was in the form of diatom frustules, commonly Navicula sp.. Large areas of the shallow water delta sediment was stabilized by a prolific growth of blue green algae belonging to the Oscillatoriales. The ability of these filamentous algae to migrate towards light prevented the colonies being buried by subsequent sediment deposition. During periods of rapid photosynthetic activity large gas bubbles were formed which became trapped amongst the filaments. Consequently, areas of the algal mats became buoyant and floated off into deeper water where constant agitation by wind generated turbulence of the lake waters, shook free the bubbles, which led to the eventual sinking of the algal/sediment pads. Thus any sorting of sediments that might have occurred due to the physical processes of deposition tended to be destroyed.

A pH of 6.8 was measured for this upper oxidized layer of the sediment (table 4). No crystaline iron minerals were detected by X-ray diffraction studies and one is led to the conclusion that most

stream and delta sediment is similar to that described by Coey and Readman (1973) namely $Fe(OH)_3.nH_2O$. Sheaths of the iron bacterium Sphaerotilus sp. were abundant in both stream and delta surface sediment and are figured in Muir, Hamilton, Grant and Spicer (1974).

Approximately 1.0 cm below the surface of the sediment the colour changed from orange-brown to black indicating a change from ferric to ferrous iron. Sediment collected from the bottom of the lake was also black in colour, suggesting anaerobic conditions for at least part of the lake bottom. No Sphearotilus or diatom frustules were found in the black sediment of the cores and only occasionally were the degraded remains of blue green algal sheaths present. The sediment was extremely fluid down as far as the second leaf bed (approx. 0.8 m) where it became gel like. This change in consistancy was not associated with any visible differences in sediment composition and only a minimal drop in the water content (table 4). XRD analysis showed no change in mineral composition.

The pellets dispersed in the upper part of leaf bed 2 were apparently of the same composition as the surrounding sediment. The origin of these pellets is still in doubt. However, it is known that the lake was partially drained for some time during the reconstruction of the weir outflow about 1957. During this time the delta surface may have partially dried out. It is known from observation that, once dry, the sediment remains as hard angular pellets and does not redisperse on wetting. It is likely, therefore, that such partial drying of the delta surface may be the origin of the pellets. When the lake was reflooded, and the distributaries wandered laterally over the delta (continually changing their courses as parts of the delta subsided or channels became choked) the pellets were eroded and deposited on the unconsolidated sediment of the delta slope in to which

they sank under their own weight until obstructed by the lower leaf bed.

At a depth of approximately 1.2 m many cores passed through a sand body of variable thickness. XRD and optical examination indicated its mineral composition was similar to that of the Bagshot sands and thus it seems likely that the sand body was derived from erosion of the stream banks during flood conditions. It was hoped to determine the direction of origin of the sand body by analysis of its geometry. Unfortunately, a series of cores which had been planned for other parts of the delta could not be carried out due to damage to the rig by vandals.

At a depth of about 2.0 m the Bagshot sands were usually encountered and occasionally contained the remains of small vertical roots.

Interpretation of the cores

The sediments lying above leaf bed 2 (including the pellets) are interpreted as being deltaic sediments. Leaf bed 1 represents deposition of leaves on the delta surface by direct aerial transport from the local trees as well as deposition of the leaves transported by the stream distributaries.

Leaf bed 2 probably represents deposition of organic material on the lake bottom. It appears that the degradation of this material, in the area from which the cores were taken, was probably more or less total under normal conditions, but the comparatively rapid deposition of the deltaic sediments arrested this process before it had gone to completion, consequently some of the leaves were preserved. The roots amongst leaf bed 2 and below are the remains of aquatic plants that were growing on the lake bottom.

TABLE 4

DEPTH Metres below Sediment Surface	% Water loss on drying at 80°C	% Fe^{+++} by weight of dried samples *incomplete digestion	pH	Eh (mv)
0.0	-	-	6.8 (stream)	+1.25
0.2	83	26.9*	7.00	-4.80
0.4	85	28.1*	7.4 ± 0.2	-4.95
0.6	87	36.1	7.00	-6.00
0.8	88	32.5*	7.30	-5.00
1.0	81	33.4	7.80	-6.10
1.2	84	32.0	7.90	-5.98
1.4	79	31.8	8.05	-5.90
1.6	79	34.8	8.05	-5.90
1.8	81	21.4	7.90	-5.2
2.0	65	11.8	-	-

Water content, Fe^{+++} concentration, pH and Eh of the Silwood delta sediment as sampled from a core taken in the Typha bed.

The sand body undoubtedly represents a period of abnormally rapid deposition. As the sand was being deposited, litter from the surrounding vegetation was also washed into the lake where it became waterlogged and sank on top of the sand layer. A considerable amount of fine material must still have been in suspension, however, and as this settled out it rapidly buried the newly deposited leaves etc. Thus, it is only under these conditions that well preserved Alnus leaves are found in the cores.

Below the sand layer another leaf bed is found that, like leaf bed 2 represents the organic matter on the lake bottom that was preserved, after only partial degradation, by the rapid deposition of the sand body.

At about 2.0 metres the lake sediments are found to directly overly the Bagshot sands. Occasionally the remains of what may be described as a soil horizon are found overlying the Bagshot sands. These apparently undisturbed sands sometimes show evidence of vertical roots and which may be interpreted as the remains of the original vegetation that grew in the valley before it was flooded.

A GENERAL MODEL OF LEAF DEPOSITION IN A FLUVIO-LACUSTRINE ENVIRONMENT

Such information as has been presented so far in this thesis is of limited value if it does not reflect general principles which are likely to have operated in the past. While it is to be expected that biological factors significantly change with time, the physical and chemical processes of transport and deposition are likely to be more stable and thus robust, and therefore generalizations derived from the Silwood study should be based on such processes.

From the core data it is evident that the deltaic sediments are vertically bounded by two leaf beds. In order to explain such a phenomenon, a dynamic model of leaf deposition in a freshwater deltaic sedimentary environment is now proposed that also has important palaeoecological implications.

In a previous chapter the relative rates of leaf and sediment deposition were used to show how the variation of leaf concentration within a volume of sediment may well reflect both the hydrodynamic properties of the plant material in relation to the inorganic sediment grains and, more importantly, the distribution of the source vegetation. Utilizing this same approach it is now possible to give an example of how such parameters affecting the variations of K may be analysed (p.150).

Consider Fig. 77. A stream, laden with sediment, empties into the relatively static waters of a lake. If the sediment load is high then the stream water will have a higher specific gravity than that of the lake and a bed density current (sensu. Smith, 1975) will be formed. However, in many lakes such a condition may not be

set up and turbulent mixing of the stream and lake water will take place at the top of the prodelta slope. Whether a bed density current is set up or not, the bulk of the coarse sediment will be deposited as soon as the energy of the transporting water falls below a critical value. This usually occurs close to the stream mouth.

In an open lake situation, free from the influence of any inflowing streams, the leaves from the surrounding vegetation either fall, or are blown, on to the surface of the lake, where they may float for various periods of time during which they are distributed directly by wind or wind generated water currents. The majority of leaves will enter the water close to the banks and may be trapped by the aquatic vegetation such as reeds or Nuphar sp. pads. As the leaves sink to the bottom they will gradually form an organic rich lake bed, and, provided that leaf input exceeds leaf degradation, a potential leaf bed will form.

H.H. Birks (1973) quantitatively compared the macroremains from such lake bottom sediments with the surrounding vegetation. Although the sampling techniques could, perhaps, have been improved, an ordination of the lake bottom remains and of the surrounding vegetation types exhibited remarkable similarity, which suggests that the potential fossil content of lake bottom sediments does, in fact, reflect the local flora. Likewise, from the delta surface leaf trap data (Table 2) it is clear that the majority of leaves falling directly on to the lake are of local origin.

Along any line running parallel to the shoreline, the deposition of leaf material by means of direct aerial transport from the local vegetation is likely to be more or less uniform, since all points along the line are equidistant from the source. Fig. 77 depicts a vertical section through the delta parallel to such a line and normal to the

delta front. The rate of inorganic sedimentation is very small in the lake by comparison to that of the rain of local plant material. The relative sedimentation rates may be represented by the length of the two vectors normal to the sediment surface as in the figure.

If we consider sedimentation at a point A on the lake bed, the rate of leaf deposition, R_L, clearly exceeds that of the inorganic sediment component R_S such that the ratio R_L/R_S (K), is greater than 1. As the delta advances across the lake bed the lake deposits become covered by deltaic sediments. At point B, at the base of the pro-delta slope, R_S has begun to increase, while R_L, dependent on the local vegetation, remains essentially constant such that $K \simeq 1$. At point C, on the pro-delta slope, R_S far exceeds R_L and K becomes much less than 1. At the top of the delta slope, at point D, the water energy is sufficiently high to keep most of the finer inorganic particles in suspension and R_S begins to fall. However, the larger leaf fragments of sufficiently high density are deposited, along with the coarser inorganic particles, in the even higher water energies experienced at the stream mouth. Thus at point E, $R_L > R_S$ and again a concentration of leaves is produced. At point F, within the stream channel, deposition and erosion are more or less balanced although leaf deposition may become so great during autumn that the channel becomes temporarily choked.

Seasonal variation in leaf deposition may impose further pattern on this basic model. If the advance of the delta slope is sufficiently rapid, seasonal fluctuations in leaf input to the system may be preserved as variations in the thicknesses of the two leaf beds. The rapid input of leaves at this time may lead to preferential preservation of such leaves, since, although there is evidence to suggest that the breeding cycle of many aquatic invertebrates is

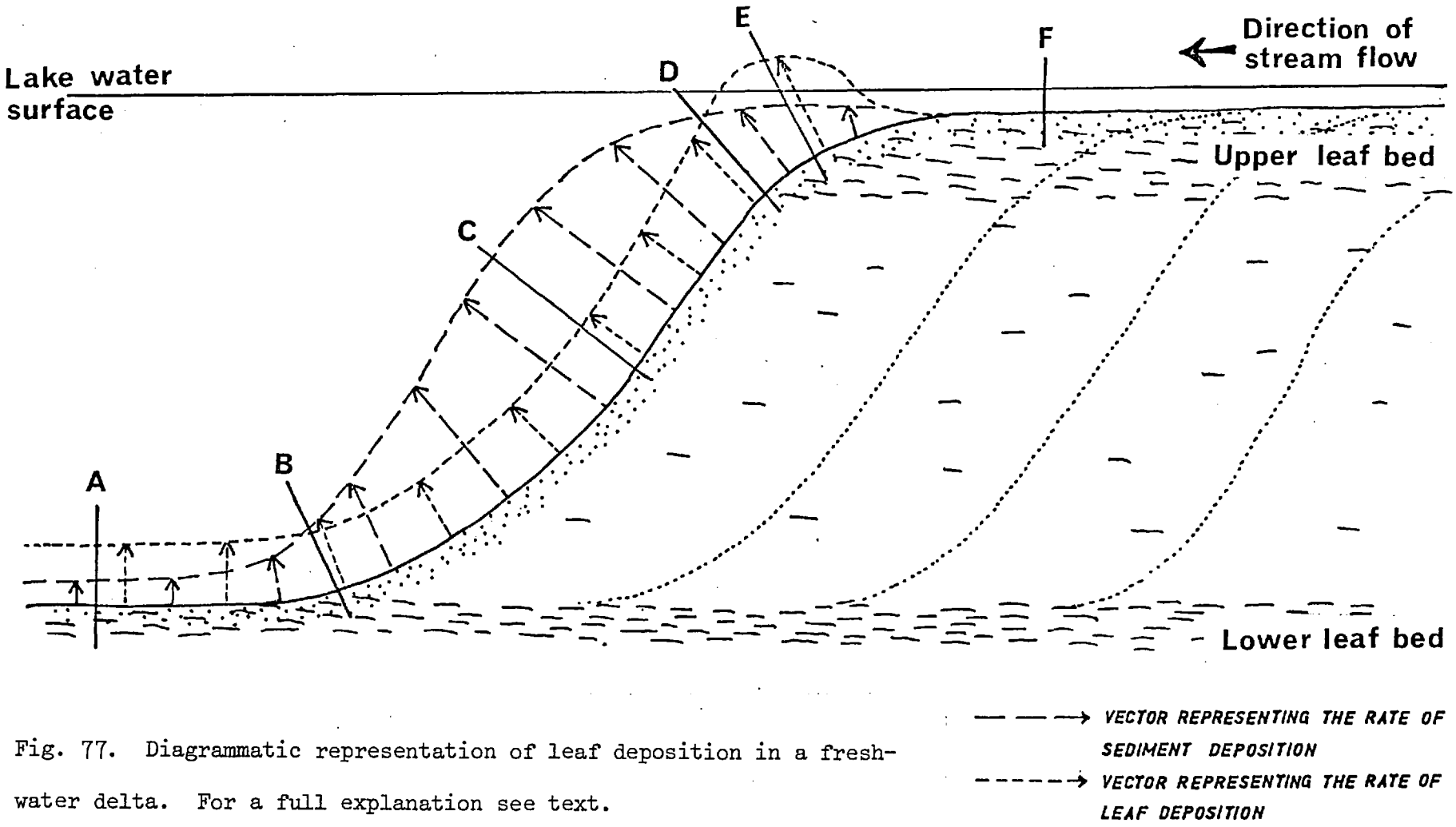


Fig. 77. Diagrammatic representation of leaf deposition in a fresh-water delta. For a full explanation see text.

linked to periods of rapid organic input (Petersen and Cummins, 1974), the population of leaf degrading organisms present in the depositional environment would not be large enough to destroy all the material before a substantial amount becomes buried.

The two leaf beds clearly have separate origins; a difference the species compositions might be expected to reflect. The local elements of the flora will be represented in the lower leaf bed and the extra local species in the upper bed. Not only will the species composition differ, but also the type and extent of degradation. The transport of the local species to the lake water surface will be predominantly by wind, thus mechanical damage will be minimal. However, in the organic rich lake bottom waters biological degradation could be considerable, and would be detectable by the characteristic rounded holes of invertebrate attack and the loss of interveinal tissue caused by microbiological activity. In contrast, the leaves of the upper bed would exhibit the angular breaks and tears associated with mechanical fragmentation during water transport, as well as some evidence of biological damage. Repeated reworking of this upper leaf bed as the distributaries wander laterally over the delta surface, will also mechanically degrade the leaf remains. Not all the leaves coming down the stream will be at the same state of saturation on reaching the stream mouth, thus any hydrodynamic properties dependent on fragment size or thickness is not likely to be observed.

Some of the leaves (most likely to be whole for the reasons discussed on page 120) will still be floating on reaching the delta slope, and will be carried off into the lake to be deposited along with the local species on the lake bed. Although small, this extra-local component of the lower leaf bed may become extremely significant.

A subjective assessment of the abundance of species within the leaf bed samples in the cores, suggested there was very little difference in species' composition between the upper and lower leaf beds. Such a situation is explained by considering the relative degradation rates of the different species as shown by experiment. The Alnus leaves were found to be very easily destroyed, compared with leaves of Fagus and Quercus. In this situation it appears that the local species are quickly removed from the potential fossil record resulting in an over-representation of the extra-local component in the lower leaf bed. Such conditions need not, of course, apply to all situations. There is no evidence to suggest, at the present time, that susceptability to breakdown is a general feature of all river or lakeside plants. Thus different parts of a flora may be under-represented.

Clues as to which floristic components were easily degraded in the past may be obtained by examining the leaf/sediment relationships. It has long been recognized that the quality of preservation of organic matter is directly proportional to the speed of burial: breakdown is retarded in the anaerobic environment that rapidly develops when oxygen diffusion is limited by overlying sediment. Such conditions prevailed at Silwood when the sand body, encountered by the cores, was formed (Figs. 72-76). After the deposition of the sand a great deal of silt and clay sized particles must have still been in suspension for some time. During this period, leaves sank on top of the sand and were rapidly buried by the settling fines. Thus it is only under these conditions that well preserved Alnus leaves were found in the cores.

Although rapid burial produces locally anaerobic conditions conducive to preservation, so does the shape and size of the lake in relation to

the input of organic matter. From Bohr's equation* (Hutchinson, 1957, p.588) it is evident that the rate of movement of oxygen across the air/water interface is dependent on the area of that interface. Thus as the area of the lake surface diminishes before the delta, the total oxygen exchange between the lake and the atmosphere drops. At the same time the ratio between the perimeter length and the lake area rises, thus there is an effective increase in organic input per unit area of the lake surface. A combination of these factors leads to an increase in the thickness of organic matter on the lake bed, although it is unlikely that there would be a proportionate increase in the more rapidly degraded species until the rate of organic breakdown was limited to such an extent that it became less than the rate of input of those species.

Such a treatment is, of course, very simplistic in that it does not take into account the oxygen production by aquatic photosynthetic organisms, or the distribution of dissolved oxygen throughout the lake waters by wind or thermally induced circulation. However, it does indicate the importance of considering the possible effects of the shape and size of a lake on floral representation.

In Fig. 77 the origin of the upper leaf bed was seen to be the result of differences in the hydrodynamic characteristics of leaves

* Bohr's equation: The exchange of oxygen through a moderately disturbed water surface into water of uniform oxygen concentration is given by the equation $\frac{dO}{dt} = A\alpha(P - pt)$

where A is the area of the interface, P is the partial pressure of oxygen in the atmosphere, pt is the pressure at which the concentration of gas at time t in the water would be in equilibrium and α is a coefficient termed the entrance coefficient.

and sediment. Clearly the magnitude of this difference will determine, to a large extent, the discrete nature and position of the upper leaf bed. The range in hydrodynamic characteristics displayed by a population of leaves, apart from any other macroremains, has already been shown to be wide and unpredictable. However, the majority of the population will fall between certain limits, and be deposited in a position on the prodelta slope where the water energies are sufficiently low so as to allow settling. The development of an upward coarsening sequence, typical of many large fluvio-marine deltas (Selley, 1971), is often less well developed in fresh water deposits due to the rapid dissipation of energy in the turbulence caused when river waters meet static lake waters of similar density. However, where there is a more gradual fall off in stream competence (such as in a bed density flow (Smith, 1975)), leaf material will be deposited along with clastic particles of similar hydraulic equivalence.

The consequences of such a model

Let us consider the infilling of a lateral lake by the progressive advance of deltaic sediments. The bottommost lake deposits might reflect the sediment load of the major river during flood, but subsequently the basin would steadily fill with macroremains from the local flora, and very little inorganic sediment. As the delta advances across the lake the upper and lower leaf beds are formed as described above. Initially, the lake is maximal in area and well oxygenated. The organic input to the lake is rapidly broken down under such aerobic conditions and the only local leaves preserved are those that were covered by the deltaic deposits before they could be destroyed. At the very beginning of deltaic sedimen-

tation, immediately after the formation of the lake, there would, of course, be only one organic rich deposit but this would soon divide into upper and lower leaf beds. The lower leaf bed might, initially, be very thin whereas the upper leaf bed would be, by comparison, rich in extra local species growing up to, perhaps, a few kilometers or more up stream.

As the delta advances, its surface becomes successively colonized by various plants and a hydrosere develops. Some of the extra-local leaves are now filtered out by new vegetation, which also contributes its own macroremains.

The developing delta reduces the area of the lake and the water becomes less aerobic, resulting in a gradual thickening of the lower leaf bed.

The final condition of the basin is shown diagrammatically in Fig. 78(a). The upper leaf bed may also thicken by secondary contributions of the hydrosere vegetation which may resemble that of the lakeside. Thus a vertical section through the infilled basin, parallel to the direction of infilling, will reveal two leaf beds. If a distance measure, D, is used to represent the species' diversity of the assemblages, it is clear that as infilling proceeds the assemblages converge (Fig. 78(b)).

If the basin is then sectioned normal to the infill direction, the bottom leaf bed will exhibit a thickening towards the basin margins, while the upper leaf bed will vary in composition laterally depending on the pattern of the distributories. To complicate the situation, the upper leaf bed will undoubtedly be riddled with roots from the hydrosere community, and the lower leaf bed, at least initially, mixed with some vegetation remains that originally grew in the now drowned valley.

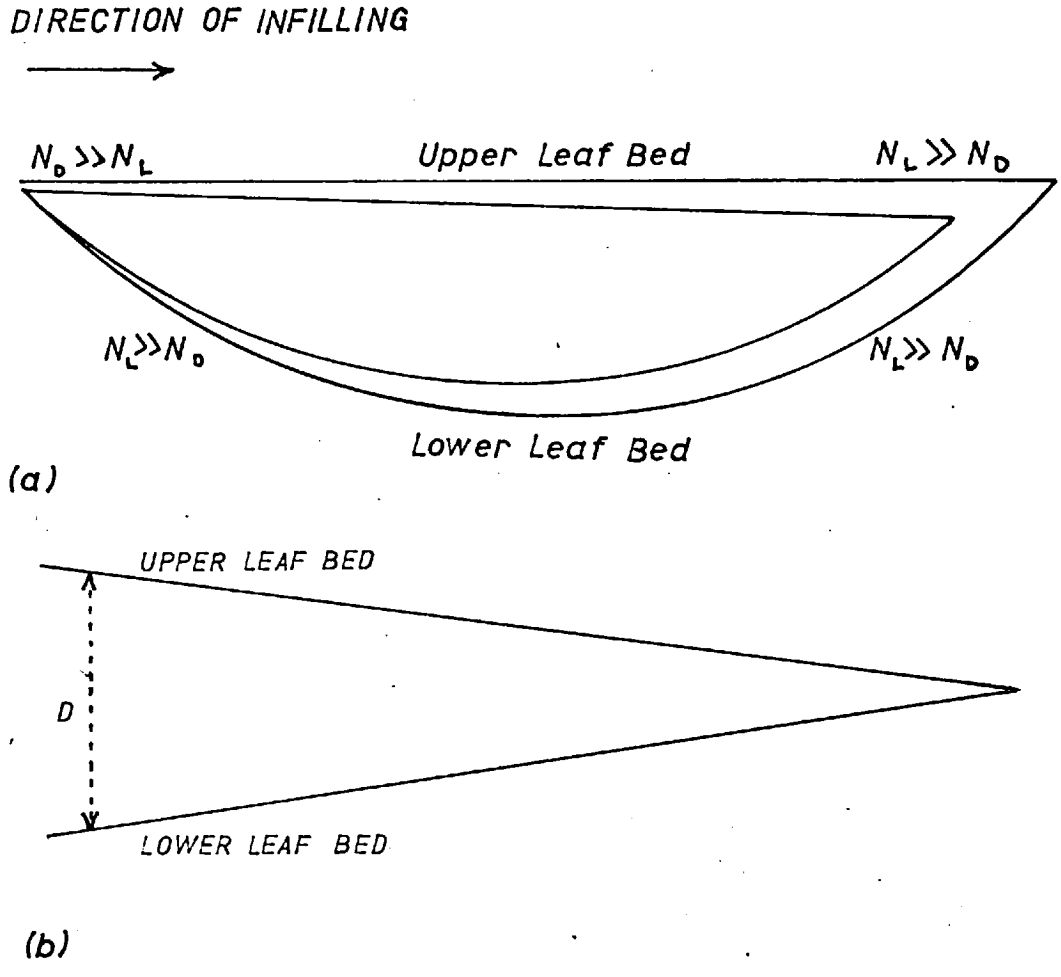


Fig. 78. (a) Longitudinal vertical section through a completely infilled lake basin. The floristic composition of the upper leaf bed changes from one dominated by a large distant component N_D in the early stages of infill, to an assemblage dominated by local components of the flora N_L as more and more deltaic deposits are colonized.

(b) If a distance measure of species diversity D is used to describe the two leaf beds, the situation described in (a) may be represented by two converging lines.

Such a simple situation is likely to be only rarely found and recognized in consolidated deposits. However, the pattern of two leaf beds, separated by comparatively unfossiliferous sediment, is a common occurrence and this model describes one way by which such a situation may arise. We shall not know what other ways there are, or their palaeoecological implications, until more work is carried out on other Recent environments. Decay and diagenesis subsequent to burial may, of course, radically alter the species pattern from what it was at deposition, but if the three dimensional structure of the deposit, and the relationship between the two leaf beds and the surrounding inorganic sediments are determined, then useful palaeoecological information may be derived. Above all, it should not be assumed that a vertical change in species composition necessarily means a change of floristic composition with time. It may, in fact, reflect changes of vegetation types in space.

QUANTITATIVE ANALYSIS OF A MIDDLE JURASSIC PLANT BED

In order to test the effectiveness of the numerical techniques used at Silwood in the analysis of fossil plant assemblages, the following exercise was carried out.

The fossil plant beds exposed at Hasty Bank (NZ 568 038) lie at the base of the Saltwick Formation of the Yorkshire Middle Jurassic and represent an extremely rich flora. The main plant bed occurs within a siltstone that was deposited in direct relation to the sandstones of a stream channel. The stream had cut into a brown micaceous claystone, also containing numerous plant fossils, and had apparently deposited the siltstones, in the same channel as it deposited the sandstones, during a period of sluggish flow (C.R. Hill, 1974). The exposure was described and quantitatively sampled by C.R. Hill who presented the data as a series of histograms in his thesis (C.R. Hill, 1974) and which are reproduced here in the appendix.

Three vertical sections were examined (Fig. 79) by excavating known volumes of rock (stands) and recovering the plant remains by careful splitting along the bedding planes. Each of the sections cut across the two main fossiliferous lithologies: the siltstone and the claystone.

The volumes analysed varied from 50 x 50 x 10 or 20 cm for the siltstone, to 25 x 25 x 10 or 20 cm for the claystone. All the larger dimensions were parallel to the bedding and contiguous samples were taken from top to bottom of the sections. Accurate density counts were recorded for the plant remains in section one by counting the numbers of fossils exposed during the course of excavation and splitting. For the other two sections the abundance was visually estimated on an

Fig. 79. Generalized section of the geology of the Hasty Bank plant bed (After C.R. Hill, 1974). The three sampled sections are shown and the positions of the stands indicated.

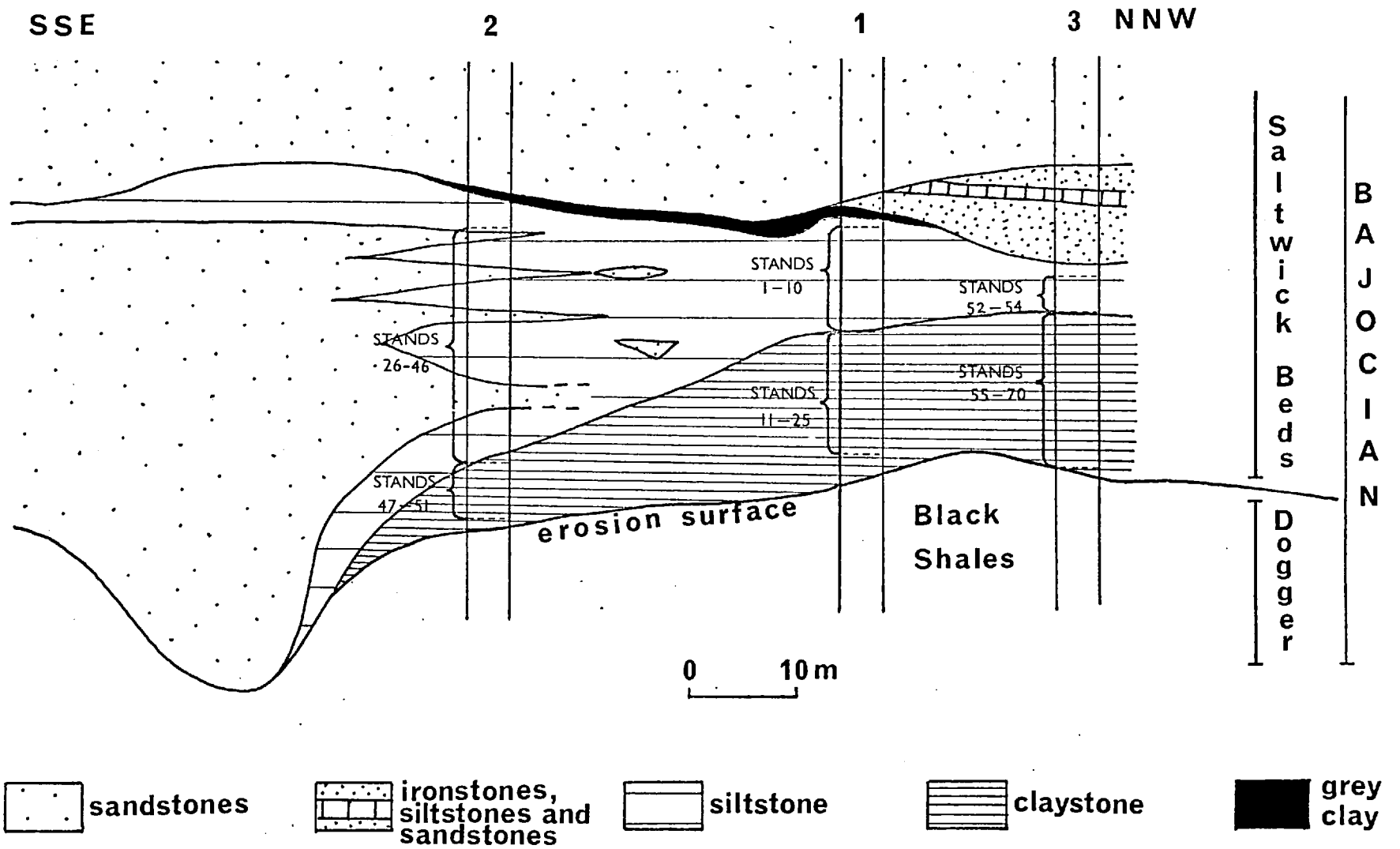

SSE
2
1
3
NNW
STANDS 1–10
STANDS 52–54
STANDS 26–46
STANDS 55–70
STANDS 11–25
STANDS 47–51
erosion surface
Black Shales
Saltwick Beds
Dogger
BAJOCIAN
0
10 m
sandstones
ironstones, siltstones and sandstones
siltstone
claystone
grey clay

TABLE 5

DESCRIPTION OF ABUNDANCE AND DOMINANCE	C.R. HILL (1974) SCALE			PRESENT SCALE	
	NO. OF FRAGMENTS	POINTS ON SCALE		POINTS ON SCALE	DENSITY EQUIVALENT
ABUNDANT Easily the most abundant species in the sample	>300	10		6	300 FRAGMENTS
ABUNDANT Occurring with other species of similar abundance	300	9			
VERY COMMON The only species of this abundance in the sample	100-300	8		5	100-299 "
VERY COMMON With other species of similar abundance	100-300	7			
COMMON The only species of this abundance in the sample	50-100	6		4	50-99 "
COMMON With other species of similar abundance	50-100	5		3	20-49 "
RARE OR LOCALIZED	20-50	4			
RARE	5-20	3		2	6-19 "
VERY RARE	5	2		1	1-5 "
A FEW SPECIMENS	1-5	1			

essentially log dominance/density scale of 1 to 10. However, as Hill points out, the concept of dominance in the ecological sense is meaningless when applied to fossil plant assemblages, thus a more suitable scheme was adopted for the analysis presented here (Table 5) based solely on abundance.

In order to compare the density information yielded by counts with those of the scaled estimates, the data from section one was analysed in both forms. The rationale behind the adoption of a log based abundance scale is derived from the assumption that a difference between 0 and 5 individuals per stand is more significant than, for example, the difference between 1000 and 1005. To test whether the logarithmic element of the abundance scale was predominantly responsible for the resulting ordination patterns, or whether the choice of scale classes was introducing an artificial weighting element into the data, the density counts were logarithmically transformed by adding 1 to all the elements of the data matrix, and ordinating the logarithms to the base 10 of the resulting matrix. In this way the original zero values were retained as zero.

To facilitate comparisons between data from different sample volumes, all the counts were appropriately weighted to refer to a sample volume of 50 x 50 x 20 cm as was done in Hill's thesis.

The data was then processed using a Q type principal components ordination and reciprocal averaging.

Discussion

As pointed out in an earlier chapter (Chapter 15) almost by definition species rich assemblages differ in more species than species poor assemblages, and it has been noted that where there are

significant numbers of species poor stands, these will ordinate in a tight bunch with respect to the others using PCA ordinations of unstandardized data (Orlóci, 1966). By inspection, the Hasty Bank data may be broadly divided into a claystone component, characterized by large numbers of species with high fossil densities, and a siltstone component which is comparatively species poor with low fossil densities. As predicted by Orlóci's observation, the PCA ordination of the unstandardized density data from Hasty Bank section 1 (Fig. 80), shows a close bunching of those stands from the siltstone and a wide dispersion of the species rich claystone stands. Although the variance accounted for by the first two axes is 67.8% of the total, the value of the ordination is limited since it is dominated by the large inherent variation linked with the species rich claystone component. The one anomalous siltstone stand (stand 9) is found to contain high fossil densities, a condition which could be brought about by a variety of agencies, including compaction.

To compensate for the response of the ordination to large variations in species abundance it is common practice to standardize the data to zero mean and unit variance by subtracting the mean of the data set and dividing by the standard deviation. Those species which occur in approximately the same abundance in all stands will have a low variance, thus they will be 'adjusted' less than those species which have a wide range of occurrences and hence a large variance. This disproportionate 'correction' of some components of the flora may, under some circumstances, be undesirable.

Fig. 81 shows the result of the PCA ordination of the Hasty Bank section 1 standardized density data. The stands plotting positively on axis II are those containing comparatively high densities of otherwise rare species such as Clathropteris obovata

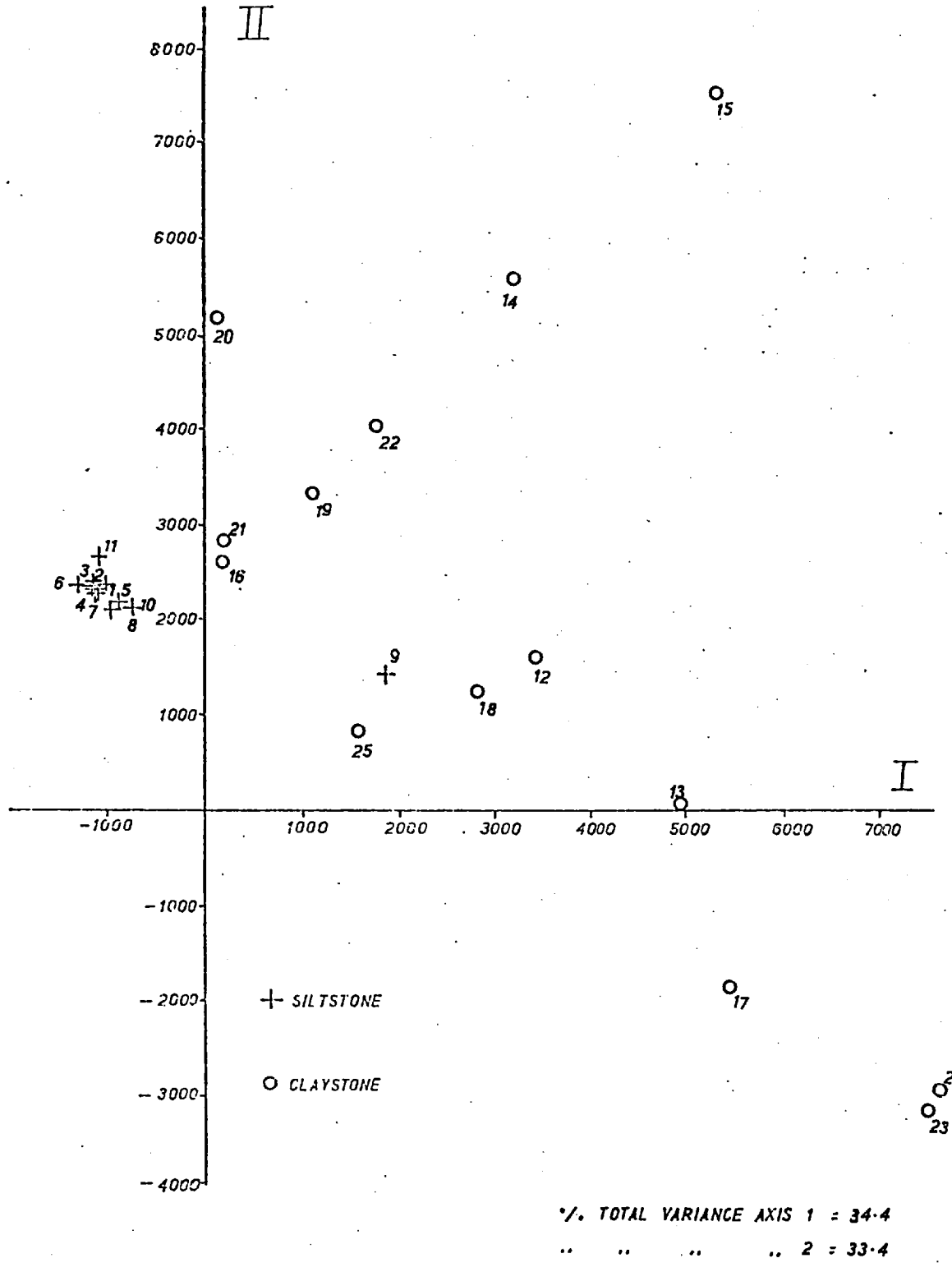


Fig. 80. Axes I and II of a Principal Components ordination of the Hasty Bank section 1 unstandardized density data. The stands are numbered 1 to 24.

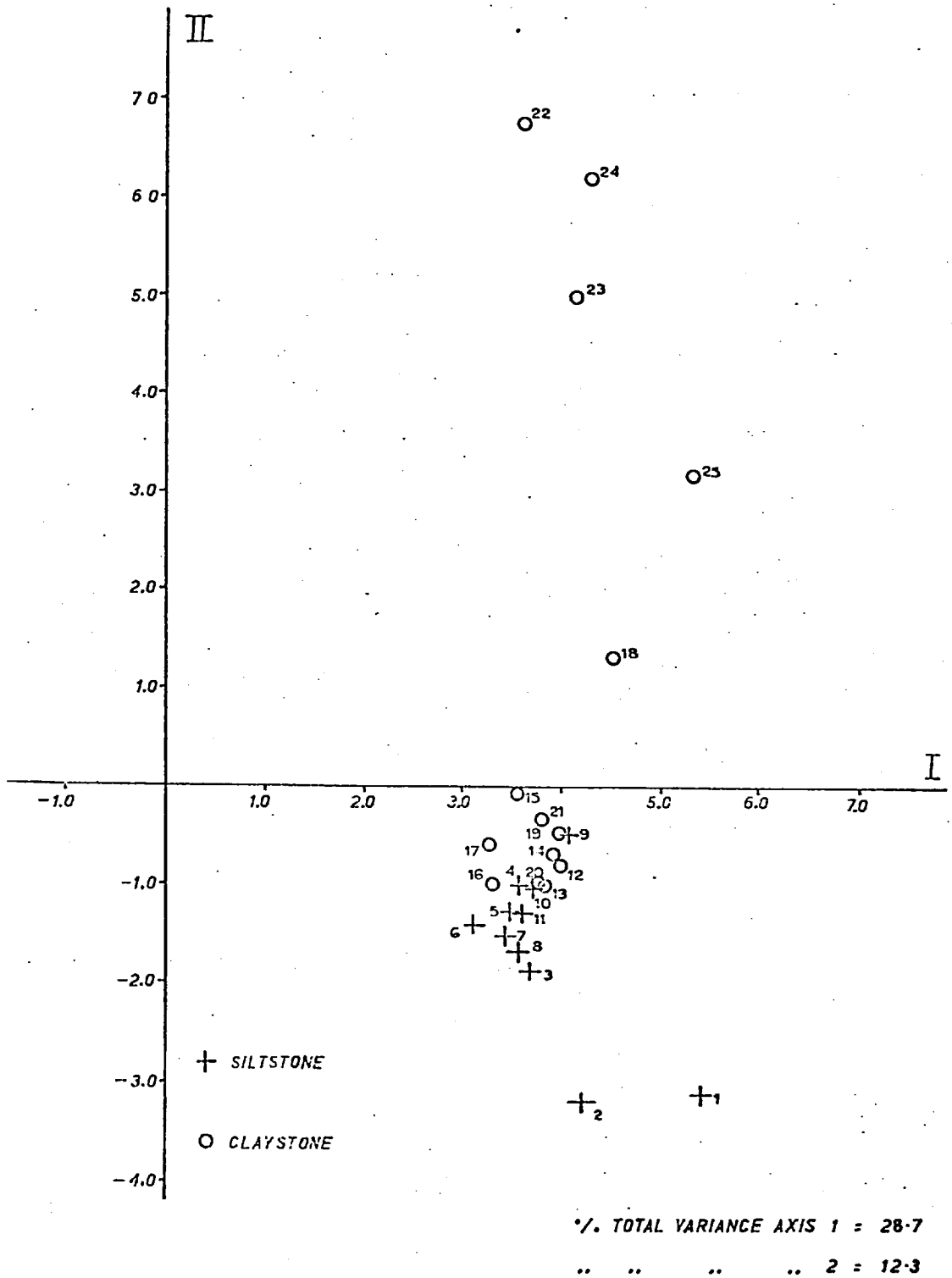


Fig. 81. Axes I and II of a Principal Components ordination of the Hasty Bank section 1 standardized density data.

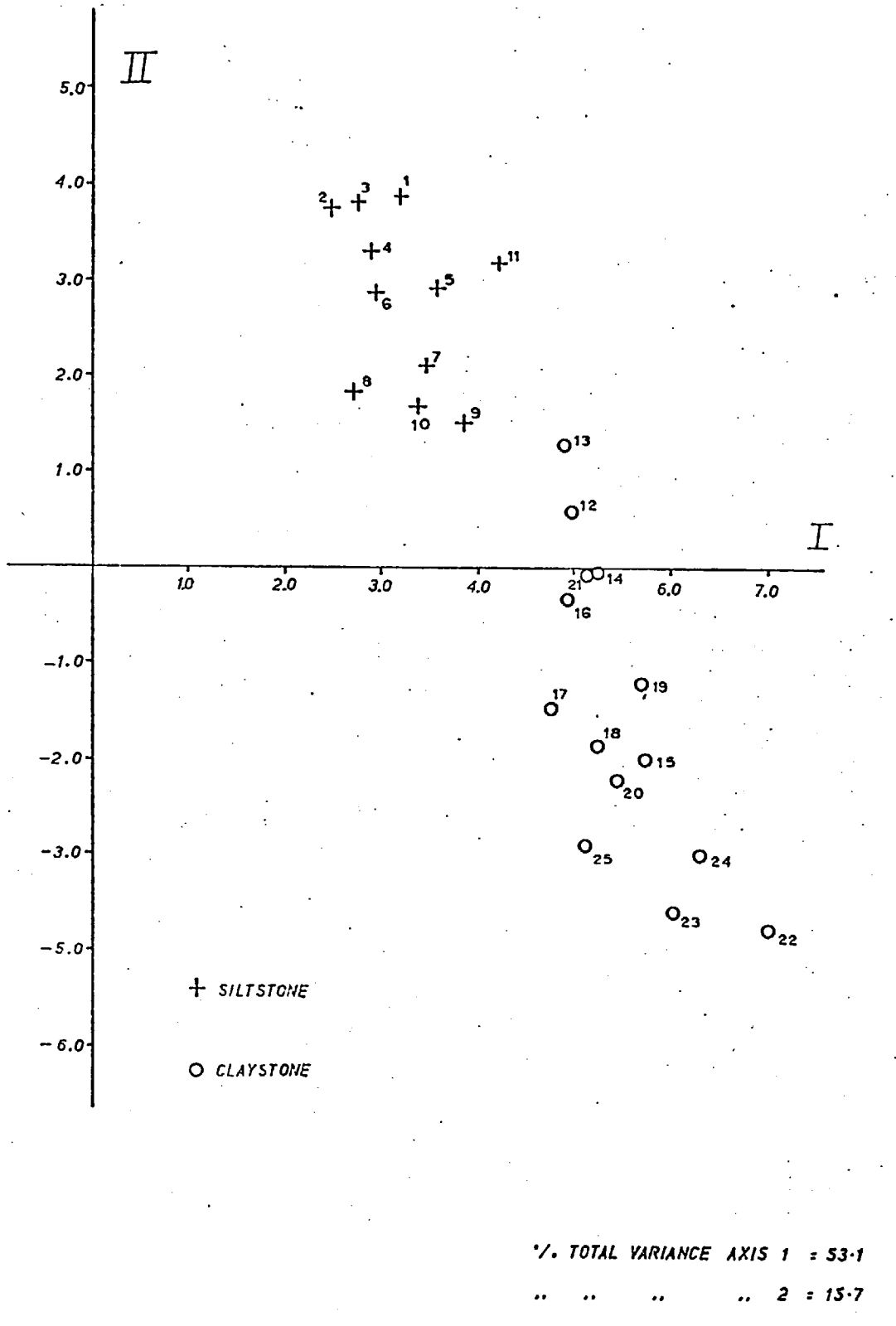


Fig. 82. Axes I and II of a Principal Components ordination of the Hasty Bank section 1 density data unstandardized, but logarithmically transformed.

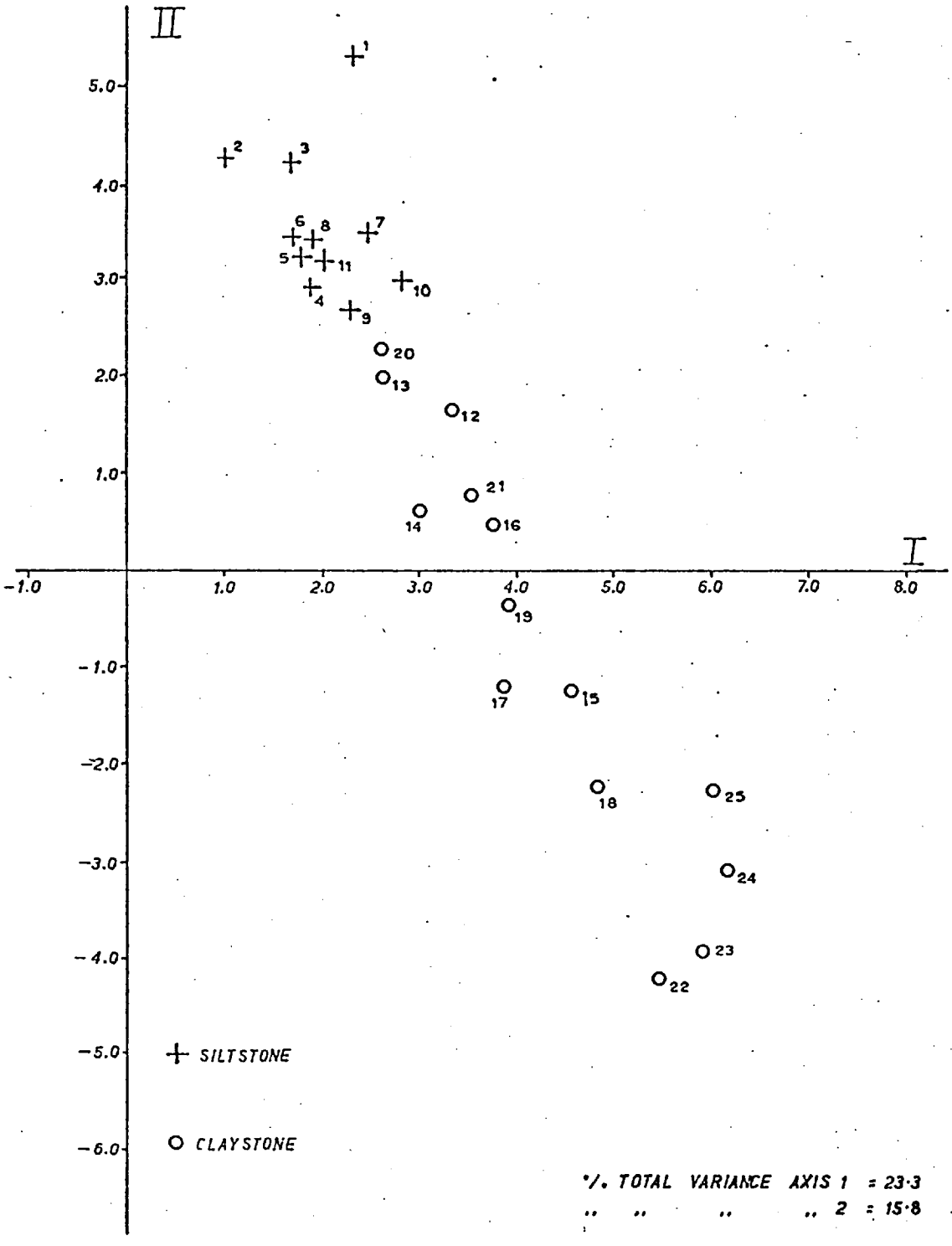


Fig. 83. Axes 1 and 2 of a Principal Components ordination of the Hasty Bank section 1 density data both logarithmically transformed and standardized to unit variance.

Oishi, Nilssonia tenuinervis Seward, Pseudoctenis oleosa Harris, Ctenis kaneharai Yokoyama, Cycadolepis hypene Harris and Bucklandia pustulosa Harris (stem) as well as the more ubiquitous species Equisetum columnare Brongniart (stems), Pachypteris papillosa (Thomas and Bose) Harris, Nilssonia kendalli Harris, Ptilophyllum pectinoides (Phillips) Phillips and Elatides thomasii (Harris manuscript name as used in Hill's thesis). In this case the separation of these stands is, perhaps, justified since they all occur at the bottom of the section and the high densities of such species may represent a real change in the assemblage. The accentuation of these stands has, however, led to a clumping of those that remain, obscuring any other information they might otherwise reveal.

By logarithmically transforming the data, the difference in scores between abundant and rare species is condensed. Thus the range of data, and the variance of the abundant species between stands, is compressed. In this way a lot of the random noise (sensu Reyment, 1969) is reduced without distorting species relationships. The effect of such a treatment of the data on the ordination is shown in Fig. 82. The scatter of points is now evenly spread, and there appears to be no disproportionate accentuation of any group of stands. Although there is a minor discontinuity between the siltstone and claystone groups, the overall effect is one of a continuum with a gradual change in species composition from top to bottom of the section. The total variance extracted by the first two axes of the ordination is 68.8%, which compares favourably with that form the standardized data (40.97%). Thus, a logarithmic transform of the data produces an ordination of the stands that may be summarized on two axes with less distortion than the ordination based on standardized data.

When logarithmically transformed data is subsequently standardized

the resulting ordination (Fig. 83) still exhibits accentuation of the stands containing high densities of the comparatively rare species, although the effect of the log. transform in evening out the scatter is still evident, and the structure of the continuum is largely preserved. The low total variance of 39.1% accounted for by the first two axes does, however, indicate that such data treatment results in an ordination that may be only poorly summarized in two dimensions.

Reciprocal Averaging as applied to the Hasty Bank data

The minimization of the 'random' variation by logarithmically transforming the data also leads to a clarification of the ordination obtained by reciprocal averaging. Figs. 84 and 85 show the results of the R.A. ordination of Hasty Bank density data. It is apparent that there is no separation of lithological types on any of the axes displayed. This conflicts with the PCA ordinations and conclusions arrived at by Hill from a subjective assessment of the histogram data. Such a direct comparison with the histograms is, however, not justified since they were drawn using data scaled on the 1 to 10 density/dominance scale. Figs. 86 and 87 show the R.A. ordination of the section 1 data after scaling between 1 and 6 (Table 5). It is immediately apparent that in Fig. 86 axis 1 separates out the siltstone stands from claystone stands, and positions those stands taken from the lithological boundary in the centre of the axis 1/axis 2 face of the plot. In many respects, axis 1 resembles the PCA ordination of the log transformed standardized data. Axis 2 displays the variation within the siltstone group and separates the top three stands (stands 1, 2 and 3) as being somewhat different from the others. Axis 3 clearly separates the claystone group into two,

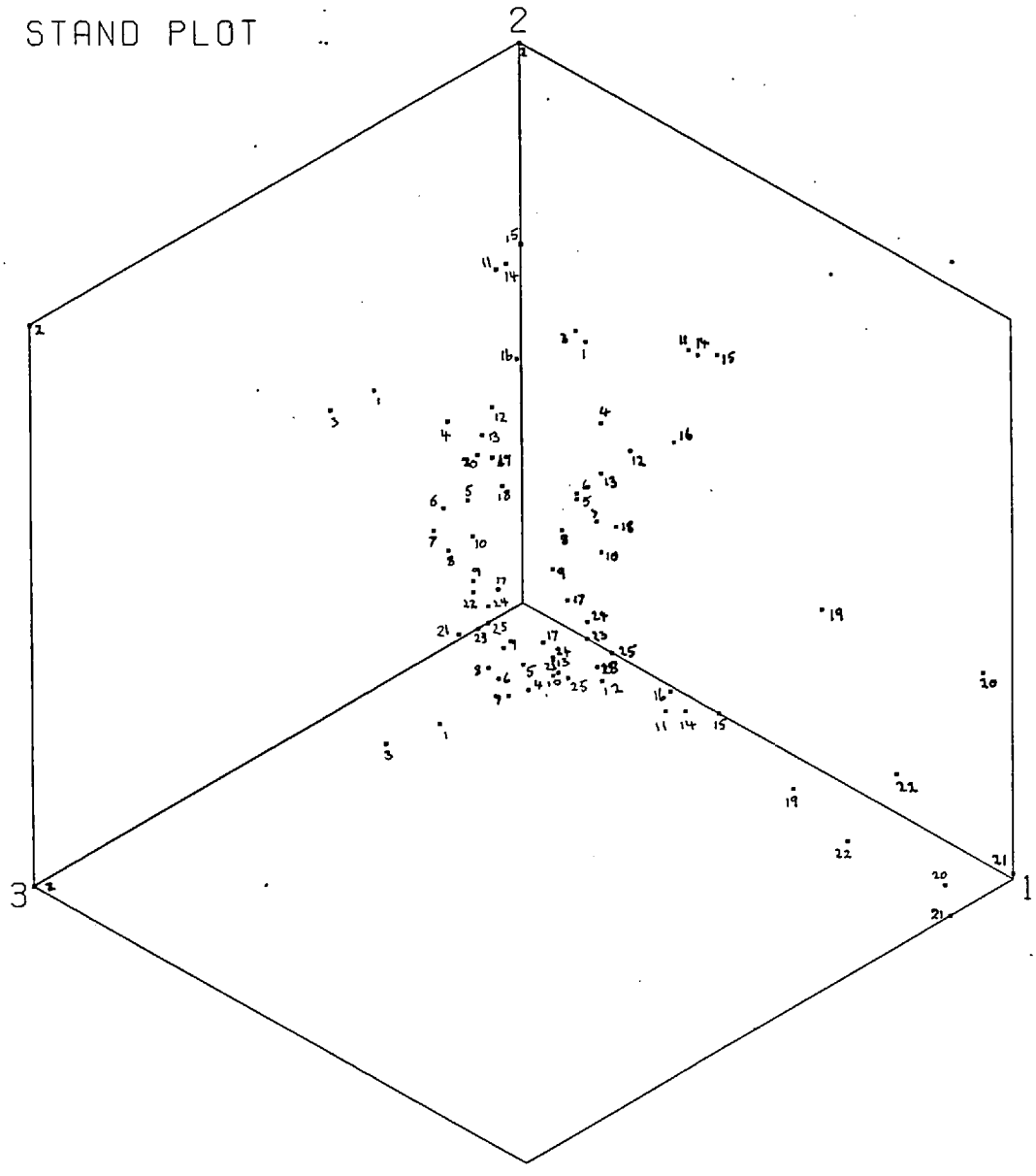


Fig. 84. A Reciprocal Averaging ordination of the Hasty Bank section 1 density data. Only the more significant stands or species are numbered in the diagrams.

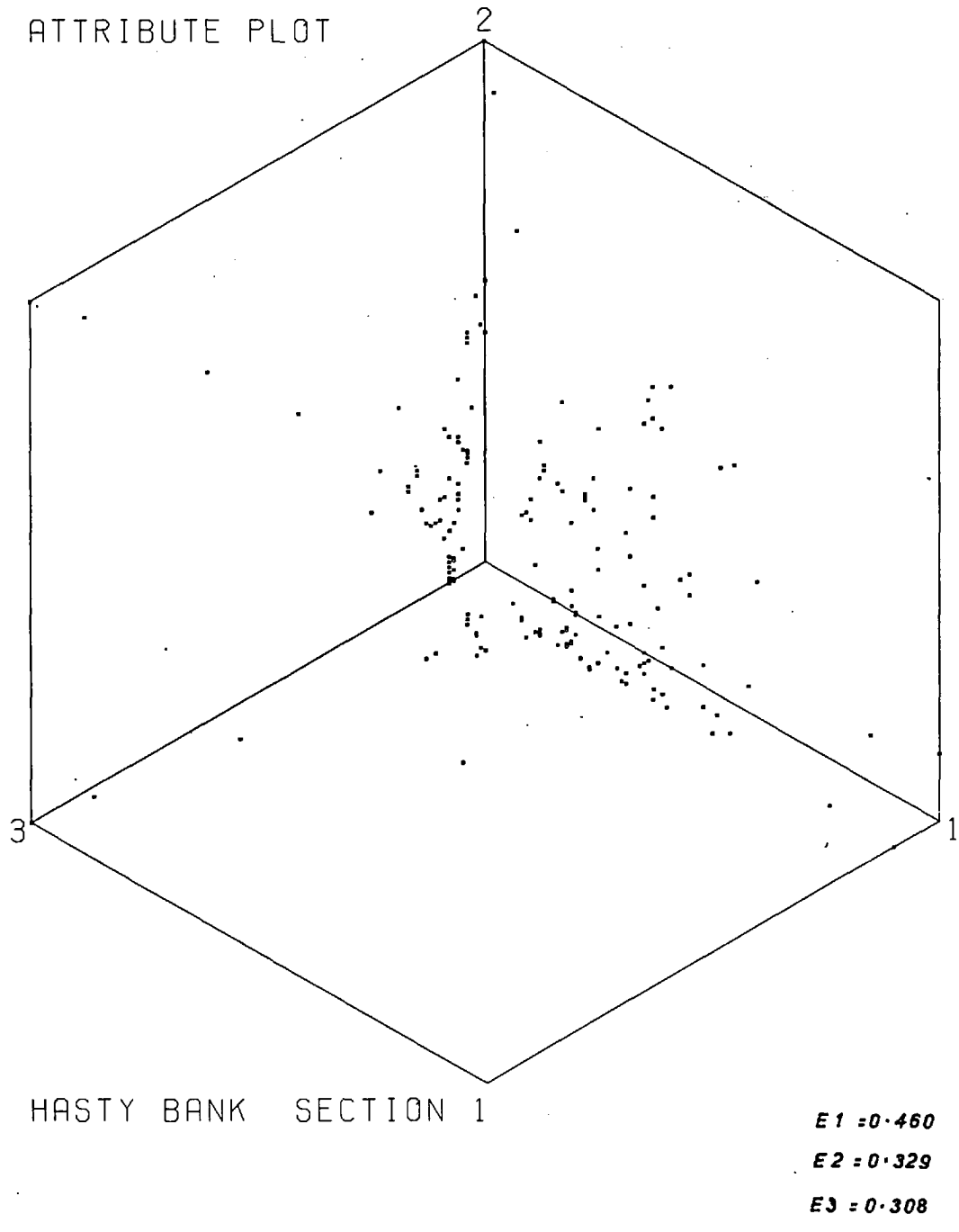


Fig. 85. The companion plot to Fig. 84.

possibly three, groups of stands characterized by three sets of species which may represent three sub assemblages.

Hill identified seven assemblages within the complete Hasty Bank sections. Assemblages I and VI were characterized by the presence of Phlebopteris woodwardi Leckenby and Pagiophyllum ordinatum Kendall respectively, and an absence of all other species. Assemblage II occurred only at the base of section 2 and was characterized by the presence of Ptilophyllum hirsutum Thomas and Bancroft and Pterophyllum thomasii Harris in addition to the species of assemblages III, IV and V. Assemblage VII only occurred in the Hasty Bank main leaf coal. It resembled assemblage II in having Ptilophyllum hirsutum and Pterophyllum thomasii but lacked Pachypteris papillosa and Brachyphyllum crucis Kendall. Both assemblages II and VII were determined from bulk macerated stands and for this reason data from them was not included in the present quantitative studies. The three remaining assemblages were designated as follows:

Assemblage V - was mainly confined to the upper part of the siltstone and was poorly defined in section 3. It was characterized by the presence of the following species.

Species identification numbers used in the ordination	
4	Marattia anglica (Thomas) Harris
18	Nilssonia syllis Harris
39	Nilssoniopteris vittata (Brongn) Florin

Assemblage IV - Intermediate between lithologies in that it occupied the lower part of the siltstone and was typified by the presence of:

37	Otozamites penna Harris

Assemblage III - Mainly found in the claystone where it is characterized by

12 Cladophlebis harrisii van Cittert

7 Clathropteris obovata Oishi

17 Nilssonia tenuinervis Seward

22 Pseudoctenis lanei Thomas

24 Ctenozamites cycadea (Berger) Schenk

47 Sphenobaiera gyron Harris and Millington*

53 Hirmerella crucis ((Kendall) Hill's manuscript comb. nov.)

48 Brachyphyllum crucis Kendall

49 B. mamillare Brongn.

These three assemblages occurred within the rock types that were quantitatively sampled and provided data for the analyses presented here.

The attribute plot of the section 1 scaled data (Fig. 87) clearly shows that species characterizing the various assemblages do, in fact, fall within those areas of the diagram designated as being representative of the various lithologies. Moreover, the species characteristic of the intermediate assemblage IV, Otozamites penna, is seen to plot midway between the lithological groups. Thus as well as reinforcing Hill's original assemblage determinations, the R.A. ordination method is shown to be a powerful palaeontological tool.

Examination of axis 3 of Fig. 87 indicates that within the claystone group there may be three sub assemblages. The most distinct of these is a

* (Harris, Millington and Miller, 1974)

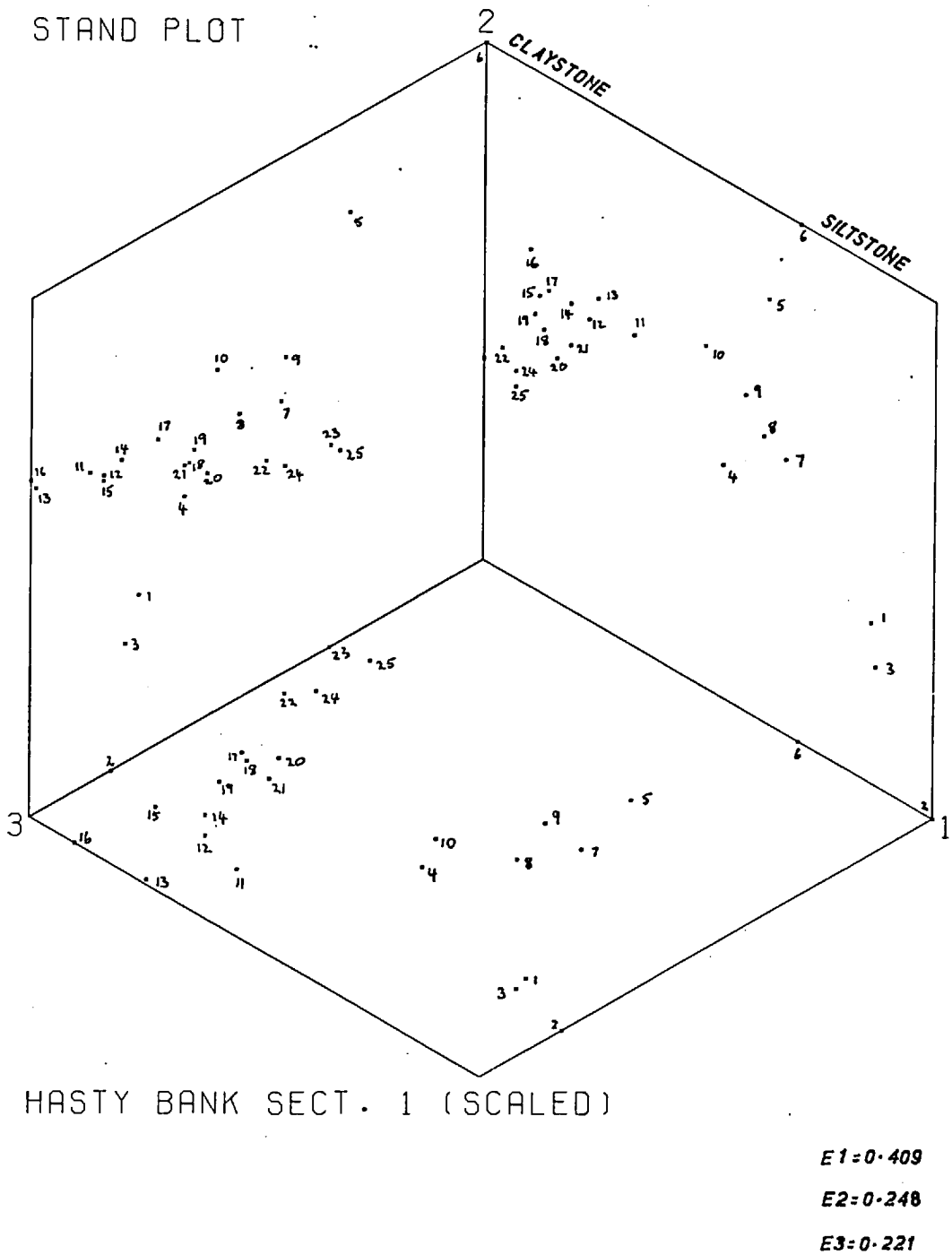


Fig. 86. R.A. stand ordination of the Hasty Bank section 1 data based on a pseudo logarithmic abundance scale. The lithological separation of the stands is clear.

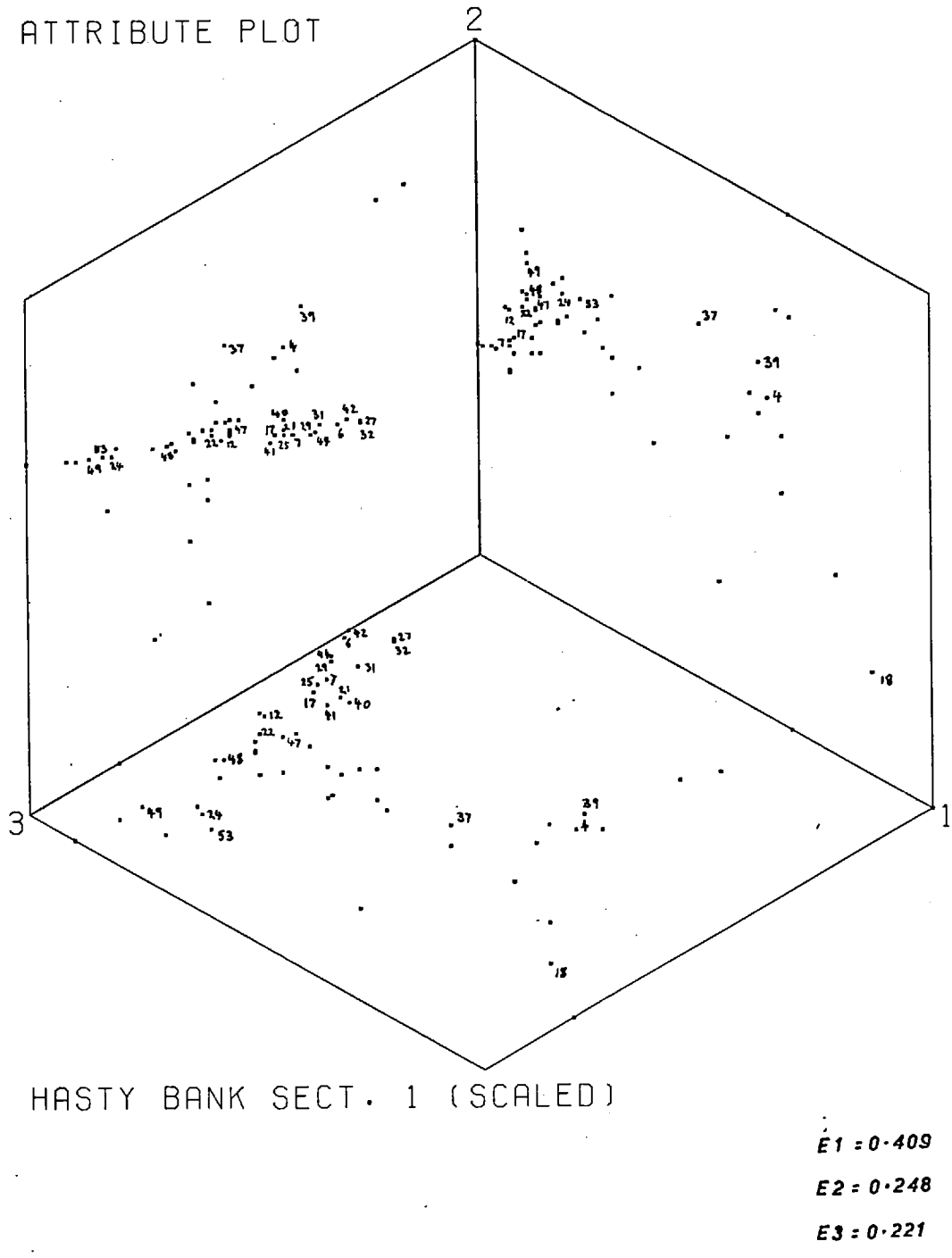


Fig. 87. Reciprocal Averaging ordination of the species from Hasty Bank section 1. The density data has been scaled according to the scheme presented in table 5.

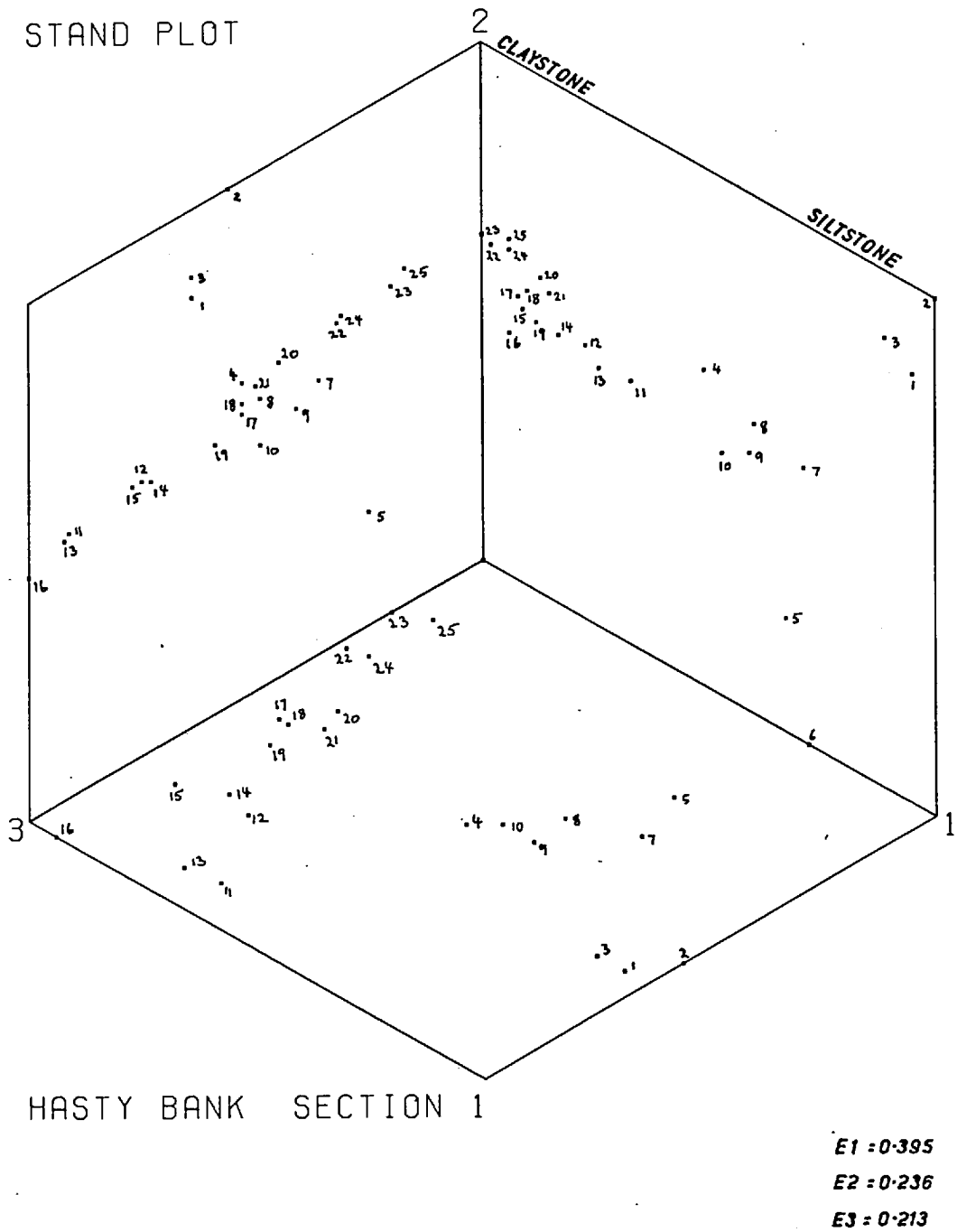


Fig. 88. R.A. stand ordination of the Hasty Bank section 1 logarithmically transformed density data. Note the similarity with Fig. 86.

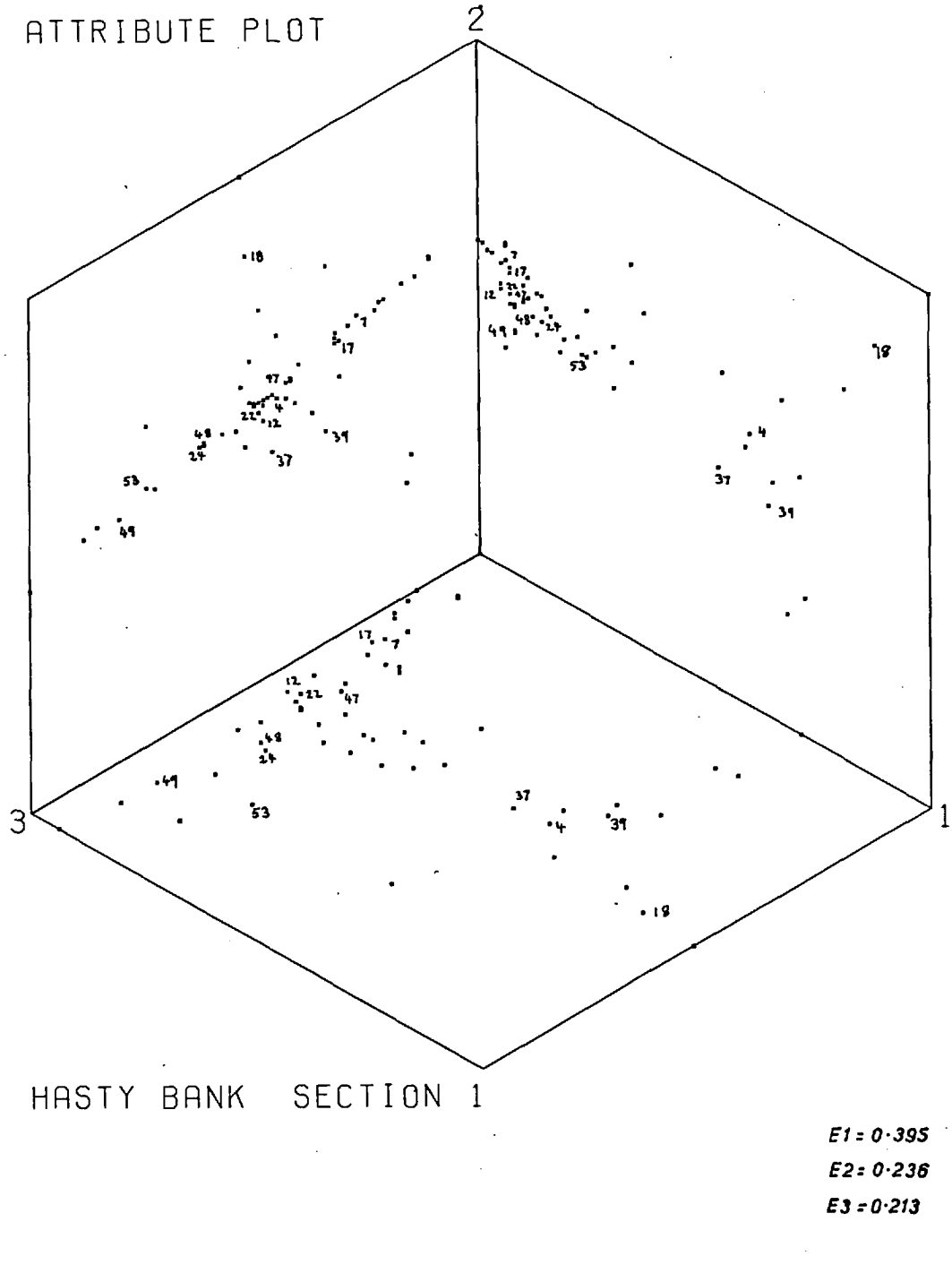


Fig. 89. Companion species plot to Fig. 88.

cluster composed of the following species:

6 Dictyophyllum rugosum Lindley and Hutton

7 Clathropteris obovata Oishi

21 Pseudoctenis oleosa Harris

25 Ctenis kaneharai Yokoyama

27 Pachypteris lanceolata Brogniart

29 Androstrobus wonnacotti Harris

31 A. major van Konijnenburg - fertile scales

32. A. major sterile scales

40 Cycadolepis hypene Harris

41 Bennettitocarpus indet. spp.

42 Williamsonia hildae Harris

44 Bucklandia pustulosa Harris

The presence of this sub assemblage is difficult to detect from the histograms but it may be seen that all of these species either occur solely in stands 22-25 inclusive, or are present in those stands in comparatively high densities.

Successful as scaling the data obviously is, the resultant ordination may be spurious if too much information is lost by the bad choice of density scale classes. If the interval between classes is not appropriate, highly erroneous ordinations could result. The extreme case of this would be a presence/absence scheme of scoring which, with the degree of 'random' variation common in palaeontological data, would frequently result in a virtually meaningless ordination. An R.A. ordination of logarithmically transformed density data is presented in Figs. 88 and 89. As can be seen, the plot is very similar to that obtained from the scaled data (although axis 2 is inverted; a condition which derives from the random allocation of initial scores in the program) indicating the suitability of the

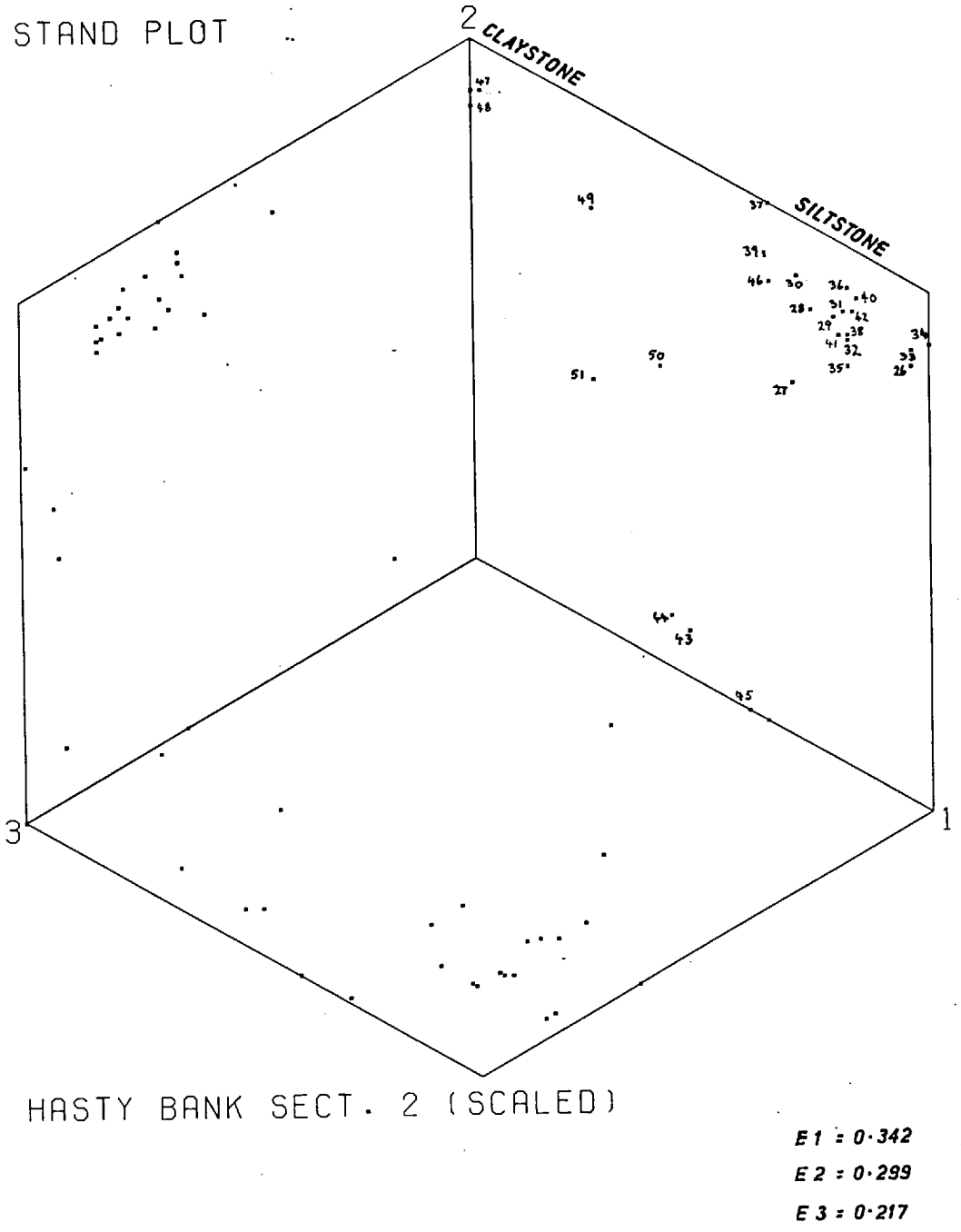


Fig. 90. R.A. stand ordination of the Hasty Bank, section 2, scaled data. Although less obvious than in Figs. 86 and 88 a lithological separation of stands may be present on axis 2.

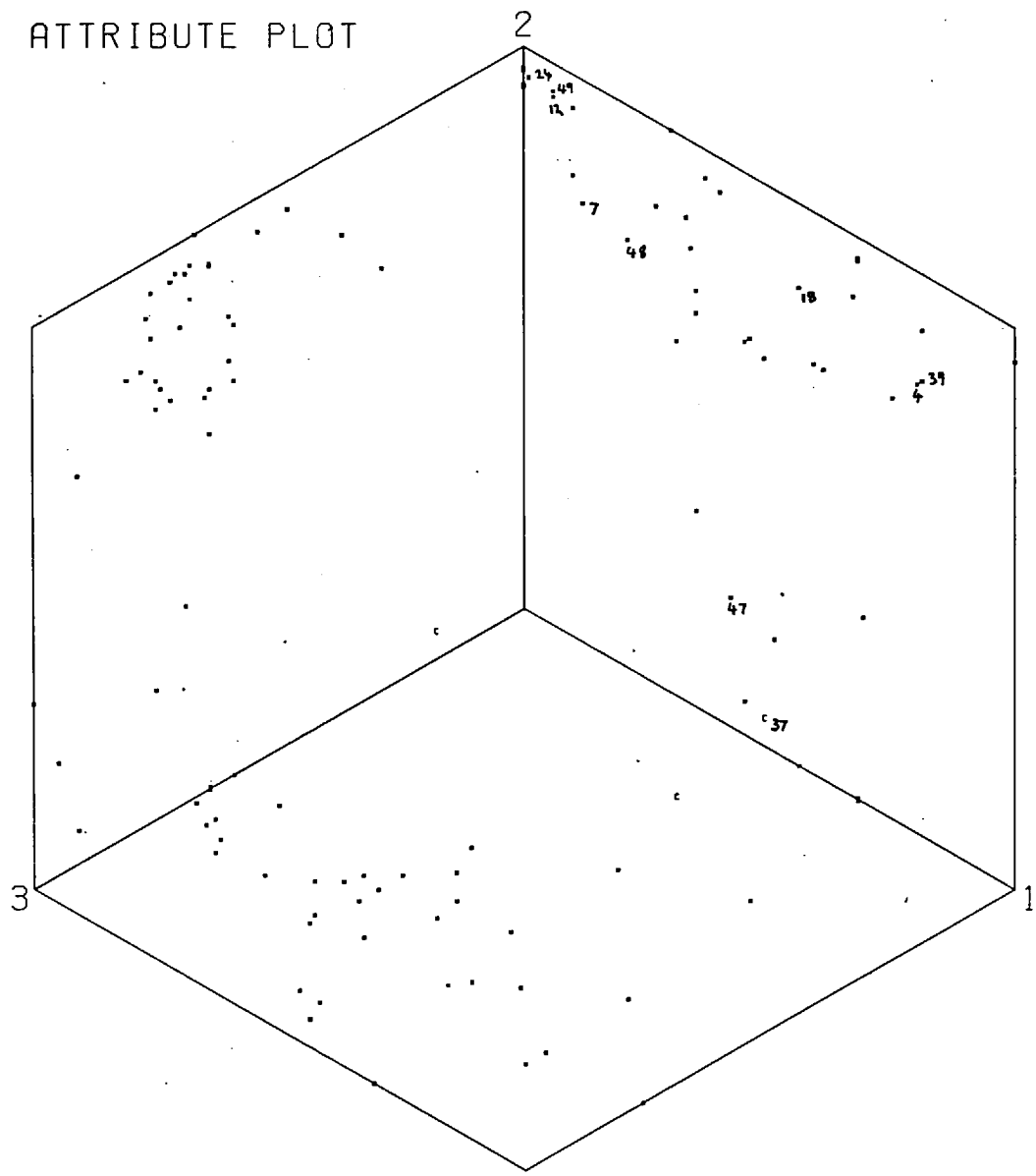


Fig. 91. Companion species plot to Fig. 90.

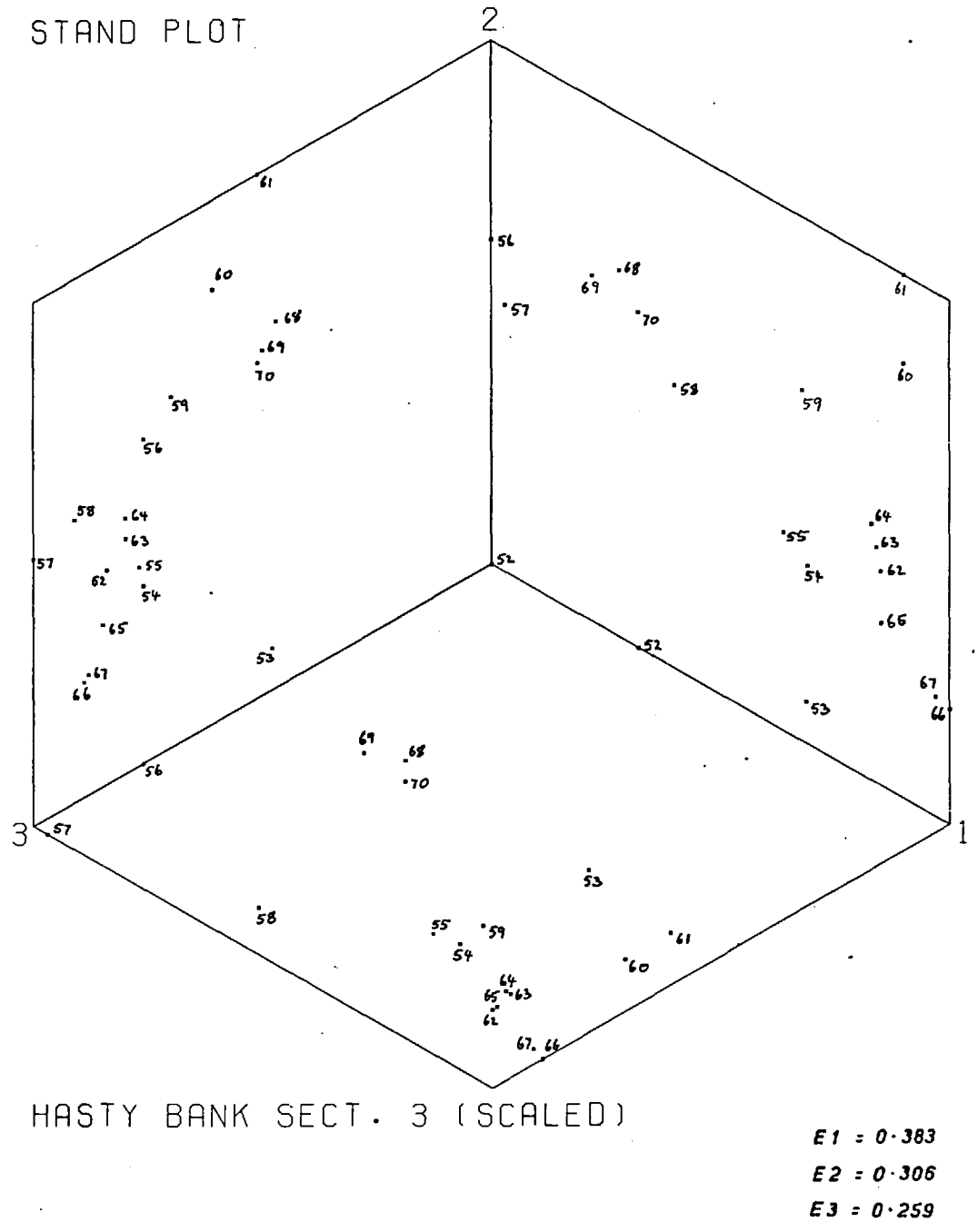


Fig. 92. R.A. stand ordination of the Hasty Bank, section 3, scaled data. No separation on lithology can be seen.

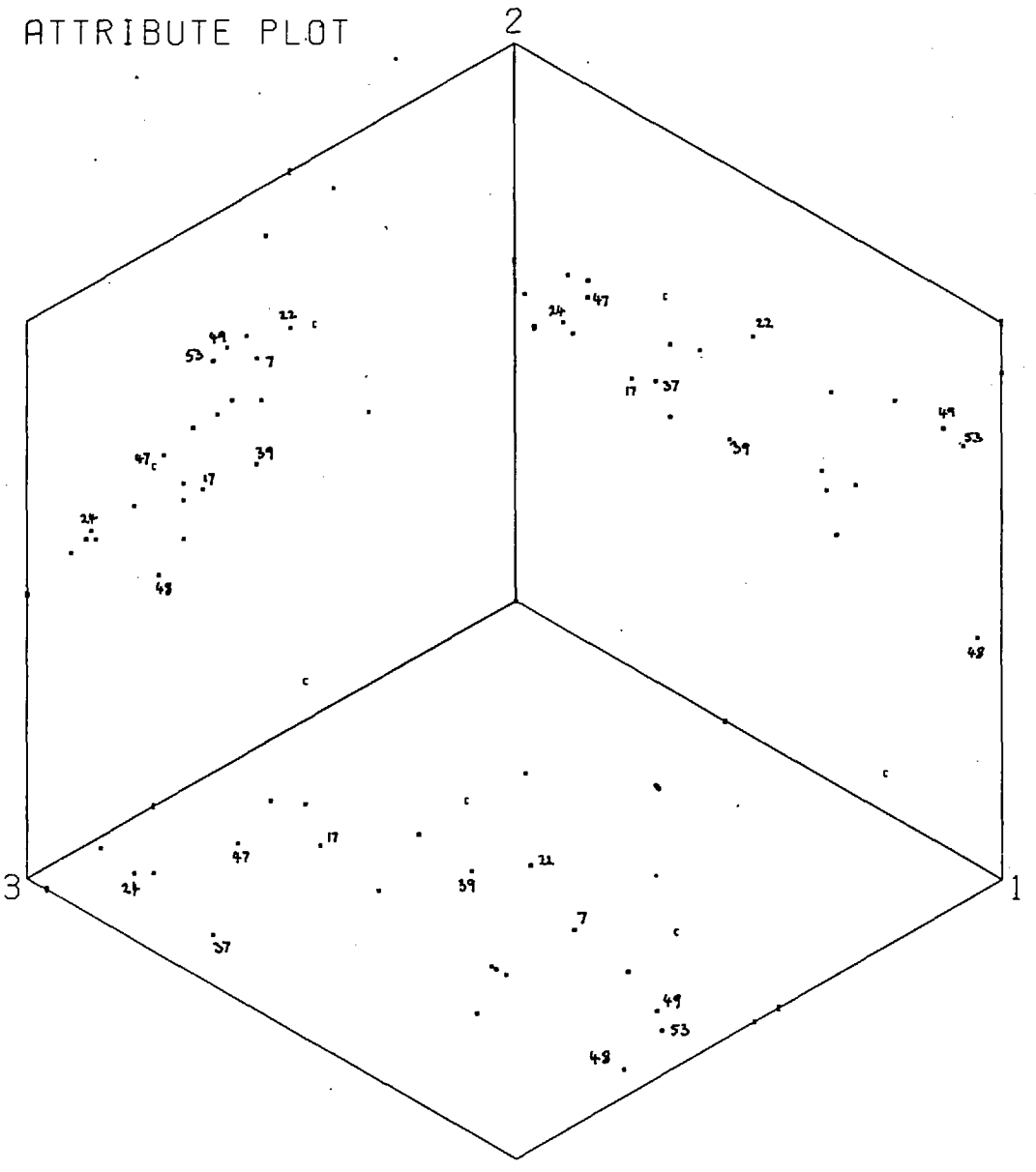


Fig. 93. Companion species plot to Fig. 92.

choice of density scale classes. Little significant information is apparently lost by the adoption of such a scaling procedure; a conclusion which has important practical consequences when sampling rich assemblages. Sections 2 and 3 were subsequently analysed by R.A. using only scaled data.

The ordination of section 2 stands along axis 1 of Fig. 90 shows a separation of the siltstone group from the claystone group with the transitional stands, 18, 19 and 20 separated out on axis 2. Stand 21 shows an apparently anomalous position, but examination of the data shows it to have a species complement similar to the siltstone, even though it is from the lithological boundary.

The attribute plot, Fig. 91, again shows assemblages largely in agreement with those determined by Hill, and once again species characteristic of the various assemblages occur within the areas of the plot representative of the different lithologies. The ordination of section 3, however, is not so clear. There are no distinct clusters or trends detectable from the plots. The attribute plot, Fig. 93, separates out Nilssoniopteris vittata, Cycadolepis spheniscus Harris and Ctenis kaneharai on axis 2, all of which are found within the siltstone assemblages of the other sections. Also the siltstone stands 1, 2 and 3 are located in a similar position on the stand plot (Fig. 92). However, while it is tempting to suggest that axis 2 may present some assemblage separation, such speculation is dubious in view of the small number of representative stands. Hill also noted that the siltstone assemblage V is poorly defined in section 3.

An ordination of the combined scaled data from sections 1, 2 and 3 shows a clear separation into claystone and siltstone stands on axis 1 of the stand plot (Fig. 94), with some of the stands at the extremities of the siltstone passing into the claystone group (stands

43, 44, 45, 46, 53, 54, 27 and 28). Axes 2 and 3 seem to account for residual variation within the groups, but cannot be assigned to any depositional or palaeoecological factors.

The attribute plot, Fig. 95, clearly separates the assemblages as did the individual analyses of sections 1 and 2. Once again, Otozamites penna (37) plots midway between the two groups on axis 1 together with root type 2.

Fossil plant material is usually highly fragmentary and only rarely are the various organs belonging to the same plant found attached to one another. The reconstruction of extinct plants has, therefore, to rely on comparative cuticular analysis coupled with consistent association between organs within the rock matrix. In the past the detection of such associations has relied on the eye and experience of the collector. Clearly, such a subjective approach may be criticised in that some apparent associations may be imaginary while real ones may be overlooked. Also, as Hill has pointed out in his thesis, any associations that do occur tend to be inadequately described. By quantitatively sampling a deposit it was hoped that such associations might be detected.

An ordination of all the available data (Figs. 94 and 95) clearly leads to a highly complex plot which is dominated by lithological controls, hence obscuring any associations that might be present. By reducing the input data to the occurrences of just one group of plants, such complications may be overcome. Fig. 96 shows the R.A. ordination of one family of plants, the Bennetttitales, for which a number of well documented reconstructions have been made. Harris (1969) gives a reconstruction of the 'Williamsonia' plant which is composed of the following fossil forms:

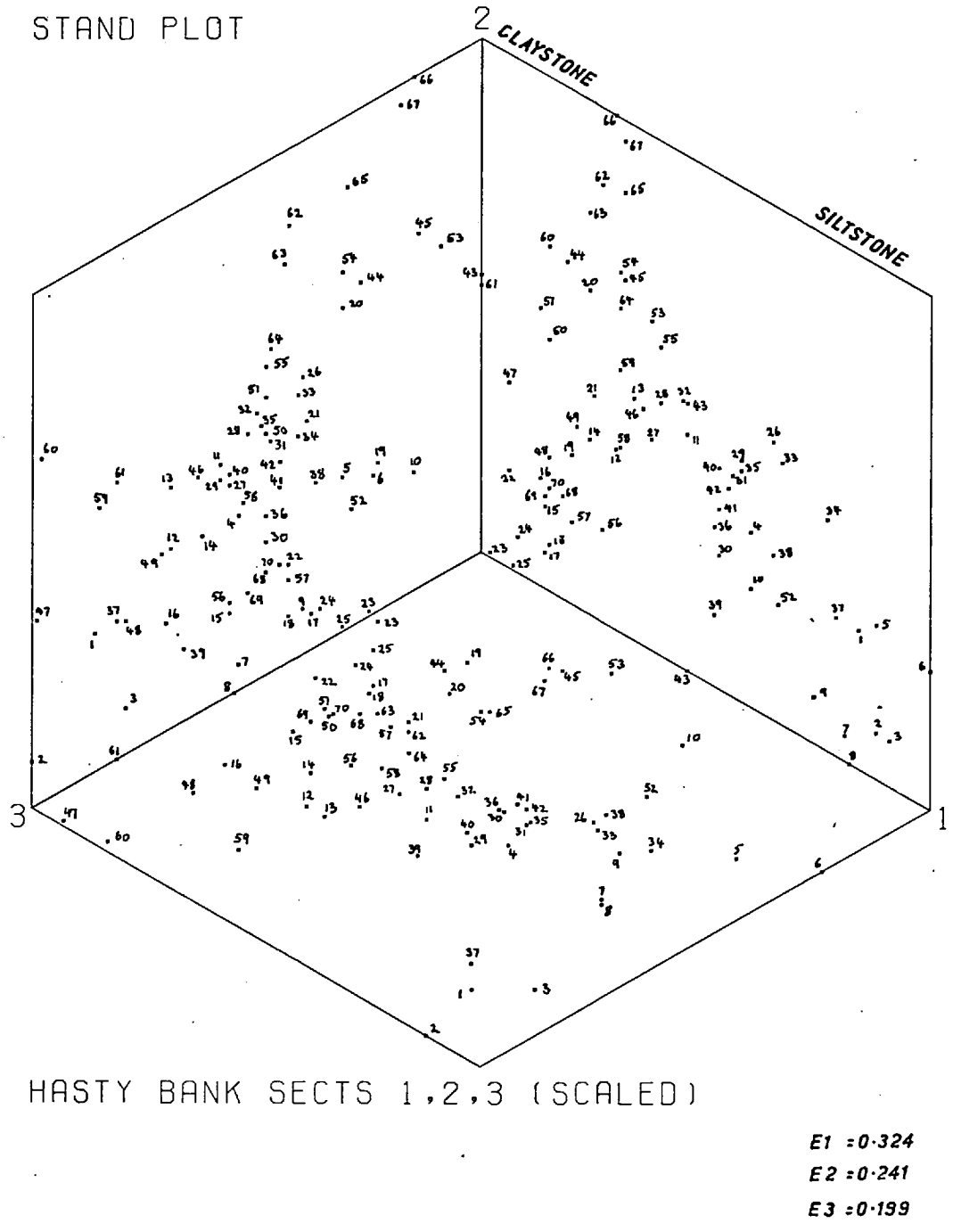


Fig. 94. R.A. stand ordination of the Hasty Bank scaled data from sections 1, 2 and 3 combined. The lithological influence is clearly seen.

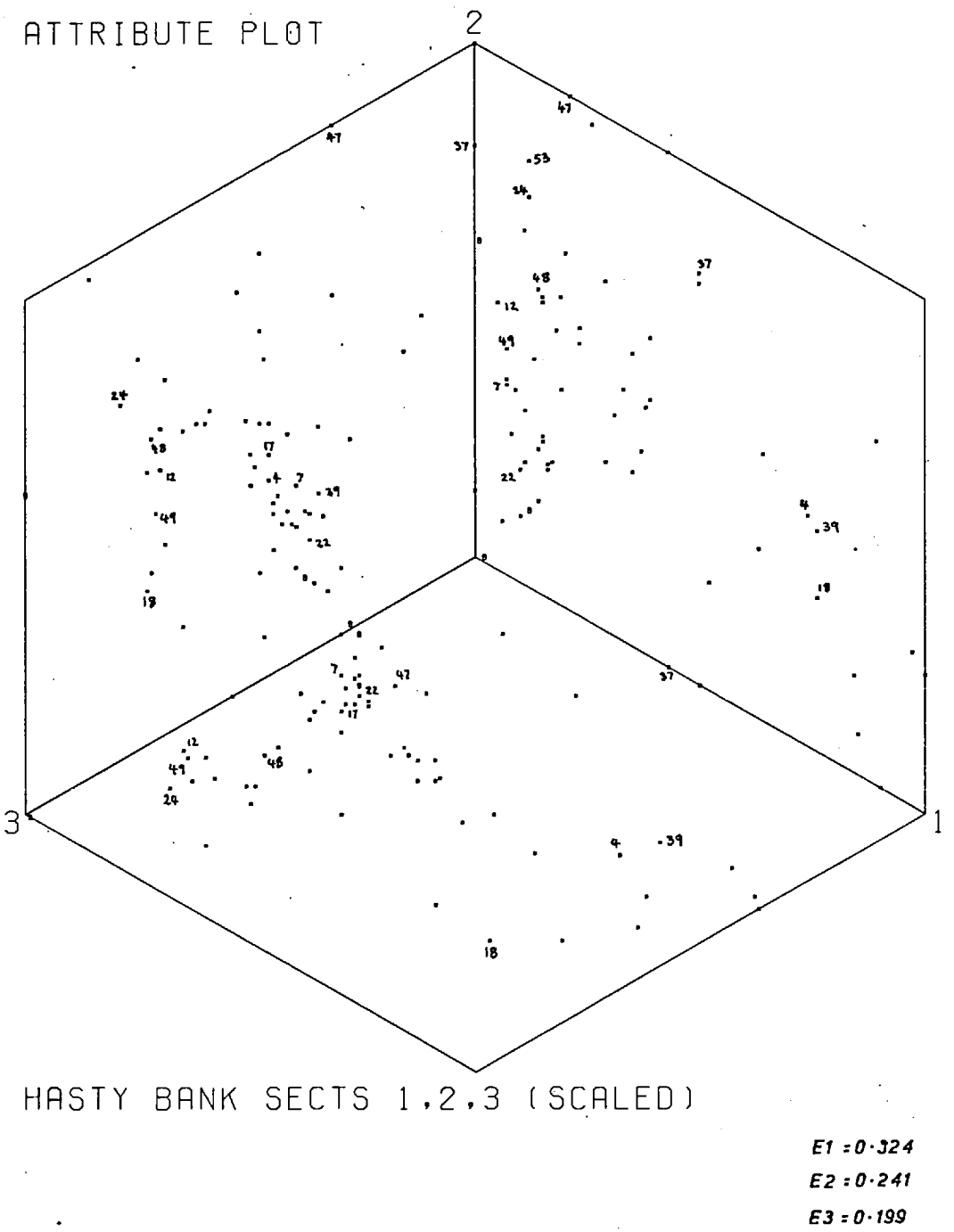


Fig. 95. Companion species ordination to Fig. 94. The positions of the species characterising the various assemblages are clearly related to the lithological ordering of Fig. 94.

Williamsonia hildae Harris (female flower)

Weltrichia whitbiensis (Nathorst) Harris (male flower)

Cycadolepis hypene Harris (perianth scales)

Ptilophyllum pectinoides (Phillips) Phillips (leaf).

Bucklandia pustulosa Harris (stem)

The evidence for linking the organs is organic continuity occasionally noted between Bucklandia pustulosa and Cycadolepis hypene or Ptilophyllum pectinoides, and the stong associations of these organs with each other.

As can be seen from Fig. 96 all these species plot close to one another except for Williamsonia hildae; the female flower. Such flowers occur comparatively rarely (only in three stands from all three sections) therefore there is likely to be a large error component in the positioning of such species within the ordination. Bennettitocarpus, the perianth scale of the female flower, does, however, occur far more frequently, and its ordinated position lies within the Williamsonia 'group'.

Cycadolepis spheniscus, Otozamites penna and Weltrichia spectabilis also show weak associations. The perianth scale C. spheniscus and the leaf O. penna plot close together, but the rare male flower W. spectabilis (only one occurrence) again plots away. The determination of this single specimen was in doubt, and when it was re-examined after the ordination had been carried out, it was considered to be more likely that it was not W. spectabilis, but W. whitbiensis. Therefore, it should belong to the Williamsonia plant in whose group on the ordination it plotted. However, with only one occurrence (as it was ordinated), its position on the plot is virtually meaningless.

If larger groups of species are ordinated, such as a combination of Cycads and Pteridosperms, the lithological control again becomes

Fig. 96. (opposite) R.A. species ordination of the occurrences of Bennettitalean plant remains from sections 1, 2 and 3 of Hasty Bank. The numbers refer to the following species:

42 Williamsonia hildae

43 Weltrichia Whitbiensis

40 Cycadolepis hypene

38 Ptilophyllum pectinoides

44 Bucklandia pustulosa

41 Bennettitocarpus

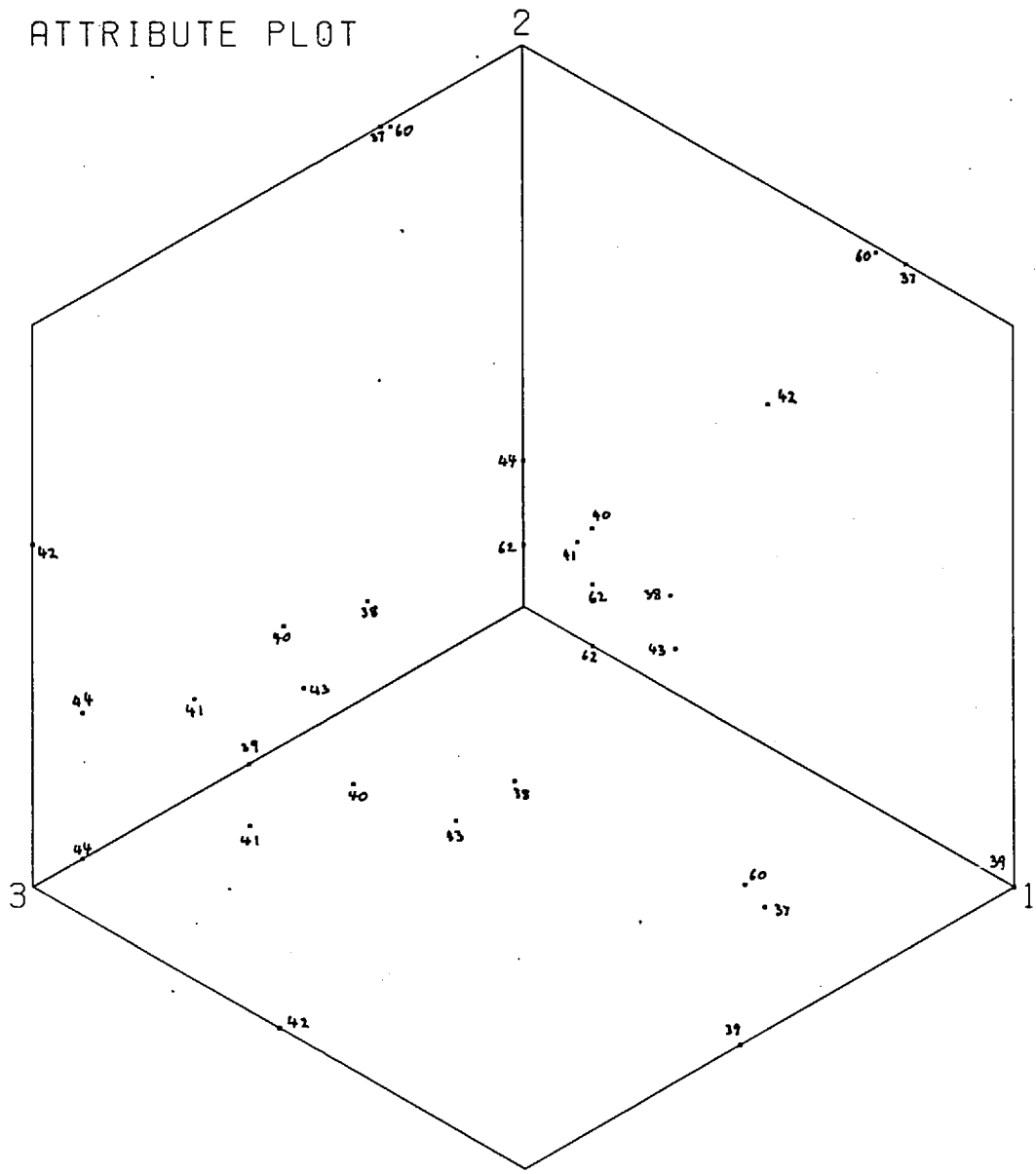
60 Cycadolepis spheniscus

37 Otozamites penna

39 Nilssoniopteris vittata

62 Weltrichia spectabilis

ATTRIBUTE PLOT



BENNETTITALES SECTS 1,2,3, (SCALED)

E1 = 0·482
E2 = 0·389
E3 = 0·301

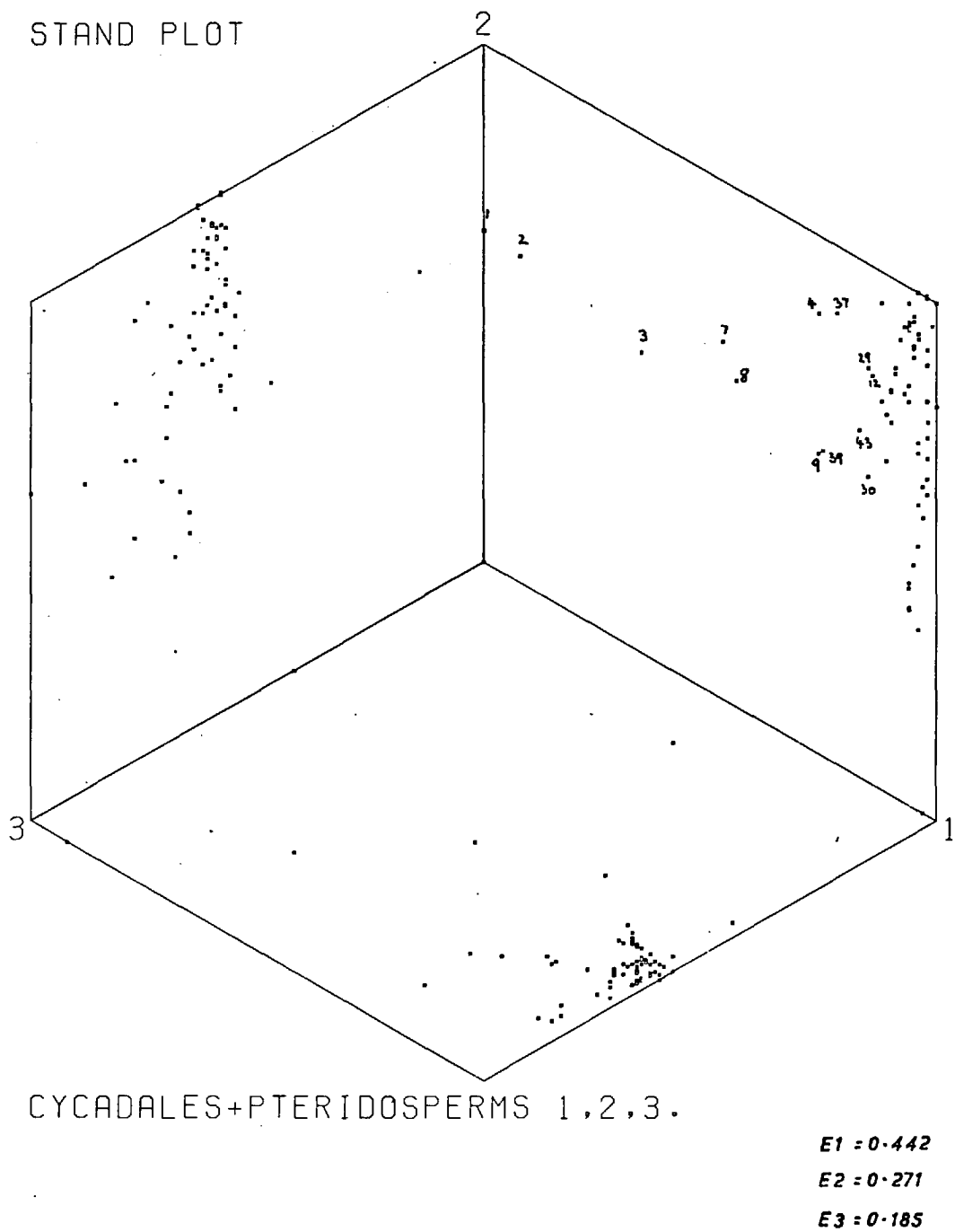


Fig. 97. R.A. stand ordination of the occurrences of Cycads and Pteridosperms in the Hasty Bank sections 1, 2 and 3.

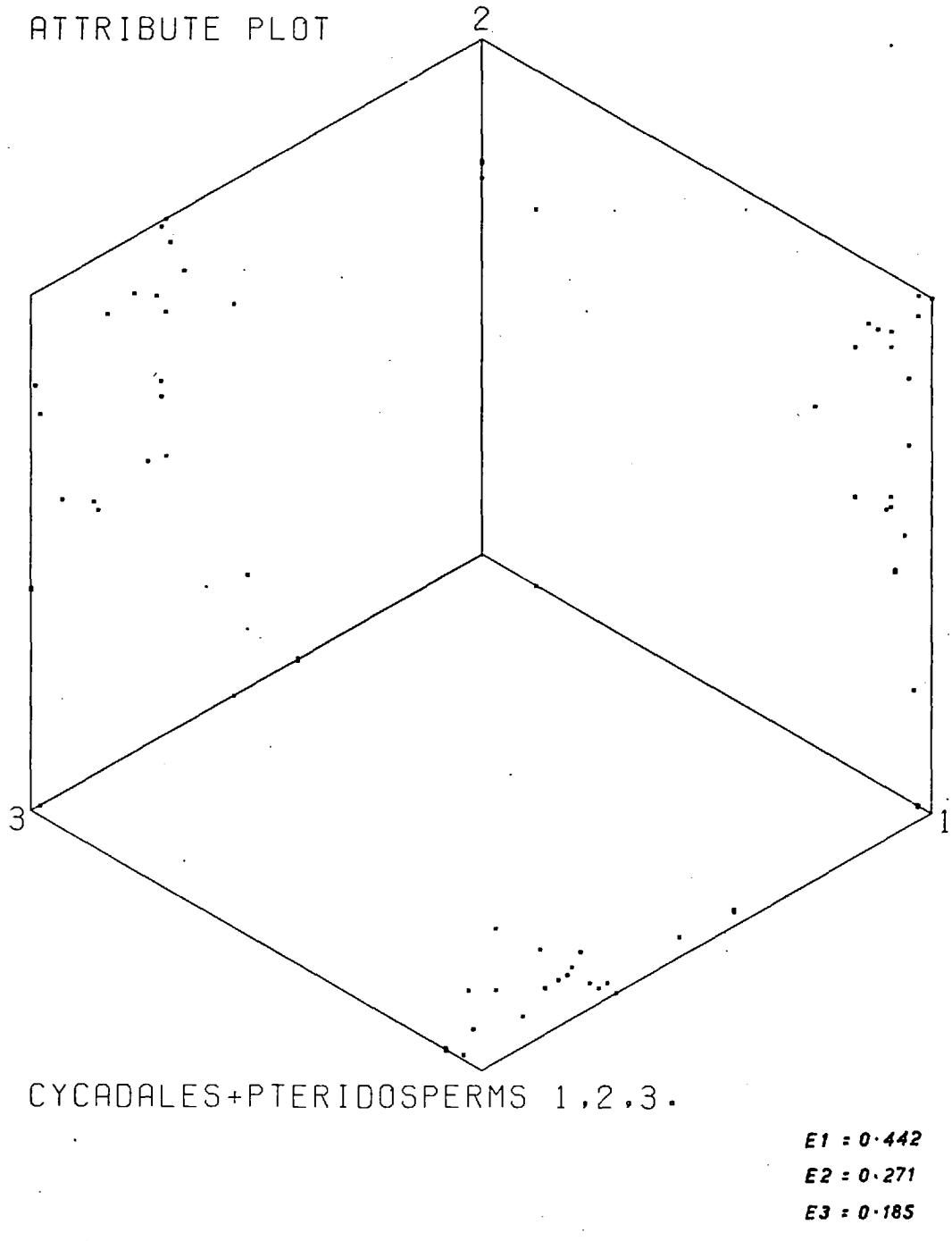


Fig. 98. Companion species plot to Fig. 97.

apparent and dominates the plot (Figs. 97 and 98).

It is evident, from the aforegoing discussion, that the R.A. ordination technique is a powerful palaeontological tool allowing rapid assemblage determinations to be made from quantitatively sampled fossil plant deposits. The scoring of such deposits may be rapidly achieved by the use of a quasi logarithmic density scale which, because the variation associated with abundant fragmentary remains is reduced, is often preferable to absolute density counts. Not only does the duality of the stand/attribute plots enable the relationship between the lithological origin of the stand and the assemblage to be readily determined, but, by appropriately restricting the data, associations between detached organs may be detected.

It is evident from the ordination of the section 1 scaled data (Figs. 86 and 87) and the ordination of the combined data from sections 1, 2 and 3 (Figs. 94 and 95) that there is an overlap between siltstone and claystone assemblages. The groups of species present in the base of the siltstone often closely resemble the claystone assemblage. Hill interprets the different assemblages as possibly being the result of successive phases of erosion and deposition within the stream channel. He suggests that a stream A originally eroded the stream channel into the claystone and then silted up depositing the plants of assemblage IV . Later a second stream B partially eroded the stream A deposits and subsequently deposited its own silts and plants of assemblage V.

An alternative, and simpler, explanation might be that only one stream eroded a channel in a partially consolidated claystone and, as it did so, it washed out large numbers of plant remains of assemblage III which became incorporated in the bottommost silts of the channel. The reworking of plant remains has generally been

regarded as being of little importance, indeed, it is often considered never to occur. However, results from the Silwood delta situation indicate that providing the plant remains are sufficiently robust, and the surrounding matrix is easily eroded, considerable reworking of macroremains may take place.

However, with the limited evidence available here, any interpretations are bound to be speculative.

DISCUSSION OF THE X-RAY MICROANALYSIS OF DEPOSITED LEAVES

X-ray microanalysis potentially provides a method by which very small volumes of biological tissue can be analysed for elemental composition extremely rapidly and more or less non destructively.

It has already been noted that leaves, on entering a depositional environment, may become coated with a layer of sediment that is extremely difficult to remove. If any attempt is made to wash the leaves, soluble ions such as K^+ may be leached and the element composition drastically altered. For wet chemical analysis, leaves are usually prepared by acid digestion and the resulting solution analysed. If this were carried out on leaves encrusted with sediment, serious errors would obviously result.

By careful positioning of the electron beam raster on a sediment free transverse fracture of a leaf, analysis of the leaf tissue may be effected with the minimum of contamination. However, X-ray microanalysis is not so straightforward as it may at first seem. This study represents an attempt to assess the method for its usefulness in monitoring the elemental changes within biological tissue during the early stages of fossilization.

Electron-Solid Interactions

The interaction of an electron beam with a solid specimen produces a variety of effects, as part of the beam will be backscattered, the rest absorbed. The energy of the absorbed beam may be dissipated by re-emission of electrons, secondary and auger, emission of light (cathodoluminescence), the production of X-rays and heat. A more complete description of these phenomena may be found in Muir (1974). Only two processes, the production of backscattered electrons and X-rays

will be considered here.

Backscattered or primary electrons are the result of backscattering of the beam from the atoms at, or near, the surface of the specimen. While these do not cause X-ray emission from the excited volume of the specimen itself, they may scatter onto the stub, or sides of the specimen chamber, and cause X-ray emission, which, if detected, is a source of spectrum contamination.

The degree of backscattering that takes place increases with increasing specimen atomic number. Most biological materials have a low mean atomic number and backscattering is therefore less than it might otherwise be.

When a high velocity electron of the beam hits an inner shell electron of an atom in the specimen and knocks it out of its orbit, a vacancy is created in the shell which is almost instantaneously filled by an electron from a higher energy level. The movement of the electron to the inner shell vacancy is accompanied by an emission of energy in the form of an X-ray photon, and the energy emitted is determined by the difference between the energy levels and thus is characteristic of the ionized element. The incident electron will usually undergo several collisions as it is slowed to thermal velocity, but at each interaction it must possess sufficient energy to knock the bound electron out of its energy level or no characteristic X-ray will be produced. Electrons interacting with the electrostatic fields of atomic nuclei radiate their last kinetic energy as Bremsstrahlung radiation, which forms the background to the X-ray spectrum and is not characteristic of the elements within the specimen. Rather the total Bremsstrahlung radiation is related to the matrix atomic number and square of the electron beam accelerating voltage, and is therefore proportional to the total excited mass of the specimen.

Specimen Preparation

Clearly when analysing the elemental composition of a specimen it is unwise to add any foreign substances during specimen preparation and yet water saturated biological tissue must be rendered stable in the vacuum of the specimen chamber. Dehydration of the tissues through an alcohol series followed by critical drying can clearly remove labile ions (Muir, Spicer, Grant and Giddens, 1974) a drawback that also applies to the preparatory procedure necessary for resin embedding. The most satisfactory method is therefore one that employs rapid freezing. If freezing is rapid enough (a temperature drop of about 100°C per second) little structural damage will be incurred, due to the formation of very small ice crystals, while the labile ions become localized. Freezing rates of this order may be achieved by quenching the specimen in Arcton '12' held at its melting point of -155°C (unless cooled to its melting point, liquid nitrogen cannot be used since it is normally at its boiling point of -196°C, and as soon as the warm specimen is plunged under the liquid a thermally insulating jacket of gaseous nitrogen is formed).

The Silwood leaf specimens were then transversely fractured under the quenching medium to expose a clean surface for analysis. It was found that if any attempt was made to cut the surface, smearing and contamination with ions and particles from the sediment crusts took place. Hutchinson et. al. (1974) and Echlin and Moreton (1973, 1974) have analysed frozen hydrated biological tissue in the S.E.M. by means of a cold stage which maintains the specimen close to the temperature of -190°C. This procedure, while retaining the tissues as close to the in vivo condition as possible, is rather elaborate and presents certain practical problems for the analysis of large numbers of specimens.

The specimen tends to act as a cold trap and measures have to be taken to prevent and monitor this contamination within the S.E.M. column. Maintenance of low temperatures throughout the specimen during analysis is likely to be difficult, unless thin sections are examined and, as stated before, sectioning the specimen can redistribute labile ions and thereby contaminate the surface to be analysed.

Freeze drying of the Silwood leaves after quenching and fracturing provided the only real practical answer to the preparation of large numbers of specimens. Although on drying, some relocation of labile ions within the specimen must take place, the movements are likely to be restricted to within each cell, and since large numbers of cells were analysed within the scanning raster on each leaf, these effects were considered negligible. Rapid freezing during quenching, and subsequent maintenance of low temperatures at the specimen, were facilitated by the use of an aluminium stub with a good thermal conductivity.

Coating

Under the influence of the impinging electron beam non conducting specimens become charged, and unless this charge is leaked to earth it can result in deflection of the beam, redistribution of loose particles on the specimen and specimen damage. Charging may be reduced by coating the specimen with a thin layer of a good electrical conductor that makes contact with the stub and thence to earth via the microscope stage. Commonly, gold or aluminium are used for coating, but these emit X-rays during the analysis that contaminate the spectrum. The Silwood leaves were therefore coated in carbon, which, although not an ideal thermal or electrical conductor, was not detected in the analysis. By restricting the thickness of the coat to the order of 300 Å (as measured by interference colours on polished brass) no appreciable

electron or X-ray attenuation occurred (Kerrick et. al., 1973).

Factors affecting the measured X-ray yields

The X-ray yields as measured at the detector may depart quite significantly from a direct relationship with the concentration of elements within the specimen. Apart from the contamination problems already mentioned, the X-ray spectrum may become distorted due to a variety of agencies. Consider Fig. 16, an electron beam impinging on a specimen excites a volume of the specimen to emit X-rays in proportion to the electron interactions with the atoms of the target. Some electrons will be backscattered onto other parts of the specimen and excite X-rays from there. Of the X-rays that are produced at the target area some may pass directly to the detector and be analysed, while others may be absorbed and possibly stimulate X-ray fluorescence. X-ray fluorescence can only be caused by X-rays of sufficient energy, i.e. X-rays of higher energy than those characteristic of the absorbing element. In biological tissue free of heavy elements fluorescence can only come from the specimen itself, or the stub, since the X-rays characteristic of the lighter elements have not sufficient energy to cause fluorescence from the heavier elements of the specimen chamber. If an X-ray does not cause fluorescence it may just be absorbed and its energy dissipated as heat. In biological material examined under high electron accelerating voltages the excited volume is large ($> 20\mu^3$) thus many of the X-rays will originate deep in the specimen, and under such circumstances most of the X-rays will have to pass through the specimen with the possibility that many will be absorbed.

Because of the complexities of electron/solid interactions and subsequent X-ray attenuation etc. it is not possible to quantitatively

analyse rough bulk specimens in the S.E.M. However, by maintaining all the machine parameters, operating conditions and specimen preparation procedures etc. as constant as possible, it should be possible to obtain meaningful comparative analyses that detect trends or changes in element concentration with treatment.

It has already been pointed out that analysing a large area of leaf reduces variables due to the migration of ions on drying etc. and, in effect, yields the average element composition for each leaf. It is commonly noted that there is significant migration of elements and mass loss from the target area of the specimen under the influence of the electron beam, and that this loss can occur within seconds of the beam impinging on the specimen, (Hall and Gupta, 1974). By using the same counting time on each analysis, however, variation between samples due to this phenomena may be reduced. Similarly, by analysing only interveinal tissue, differences between spectra due to varying specimen density etc. should be reduced to a minimum.

The Peak to Background ratio

It has already been pointed out that the background radiation is proportional to the excited mass of the specimen, and since the peak intensity is related to the number of atoms of that particular element emitting characteristic X-rays, the peak to background ratio is proportional to the concentrations of that element in the excited volume of the specimen. The mass change under the influence of the electron beam, and the fact that no two leaves are identical as regards tissue density etc., means that the total background radiation will, in spite of all precautions, vary from specimen to specimen. Under these conditions, the only suitable way of representing relative elemental concentration is in the form of the Pk/Bg ratio.

Stemming from the work of Hall (1968 and 1971), it has become common practice in quantitative microprobe analysis to compare such ratios and peak intensities with standards containing the elements of interest in known concentrations. The use of standards suitable for biological specimens presents a number of problems, however, and consequently a variety of methods of preparing standards have been proposed (e.g. Rosentiel et. al., 1970 and Spurr, 1974). However, it is extremely unlikely that the standards used will have exactly the same properties as the specimen and that the elemental concentration within the small volume of the standard that is being analysed is the same as that in the bulk standard.

In an attempt to dispense with the need for standards, methods 'correcting' spectra based on theorectical assumptions have been proposed (e.g. Warner and Coleman, 1974, and Russ, 1974). The more simple models can only be applied under certain conditions, for example, thin sections, while others require sophisticated computer programs and even then the usefulness and suitability of the methods are doubtful. It was therefore decided to make no attempt in the present study to convert the peak intensities to absolute concentrations.

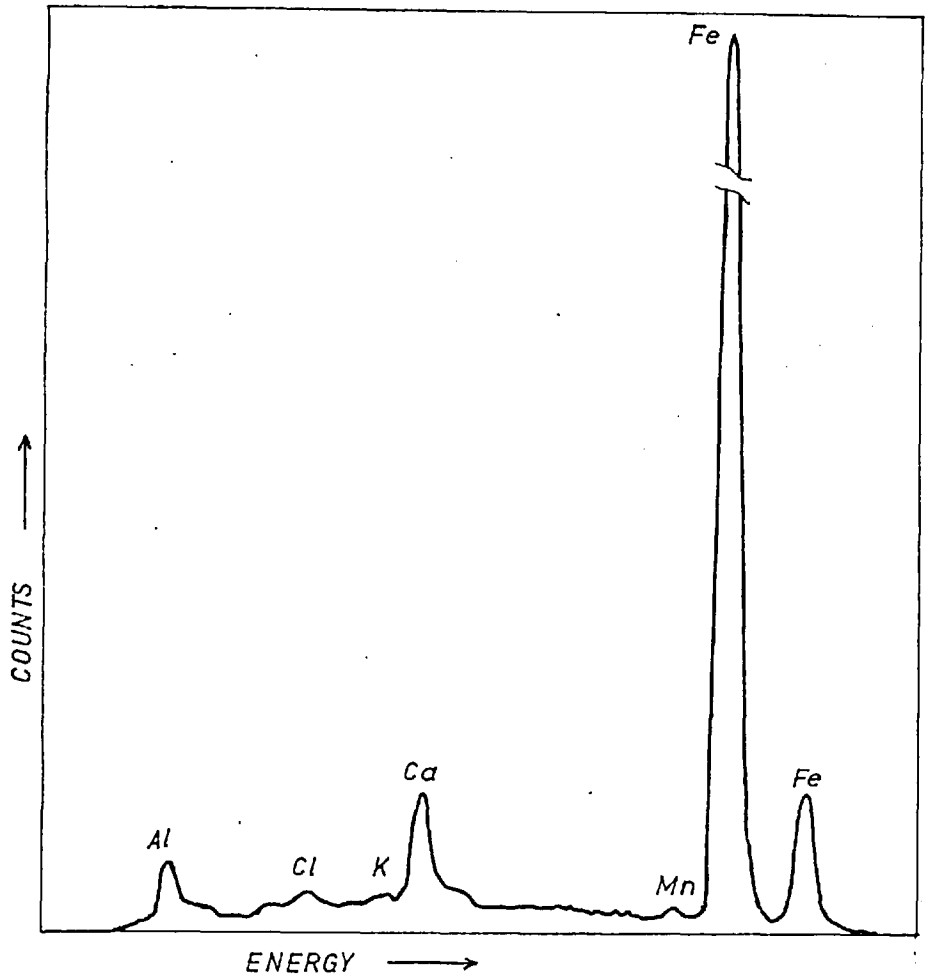
It was realized at the beginning of the experiment that large variations in Pk/Bg ratios would be observed even between replicates. For this reason it was decided that at least five replicates of each treatment needed to be analysed. However, in the course of specimen preparation, some specimens proved unsuitable for a number of reasons thus, in many cases, replication was seriously reduced. One of the most difficult stages in the process was achieving a suitable coat of carbon on the specimens. Vacuum coating was abandoned in favour of 'sputter' coating mainly because the latter process was more rapid. Neither method gave a coat that prevented charging under the beam

energies required for microanalysis. Charging of the sediment encrustation frequently resulted in small particles of sediment moving and being deposited on the clean fracture surface that was being analysed, leading in some cases to severe contamination. Such analyses were discarded. The elimination of these doubtful results inevitably led to large gaps in the data and, such results as there are, have become largely inconclusive. However, the potential of the method is demonstrated in Figs. 99-103 which will now be considered.

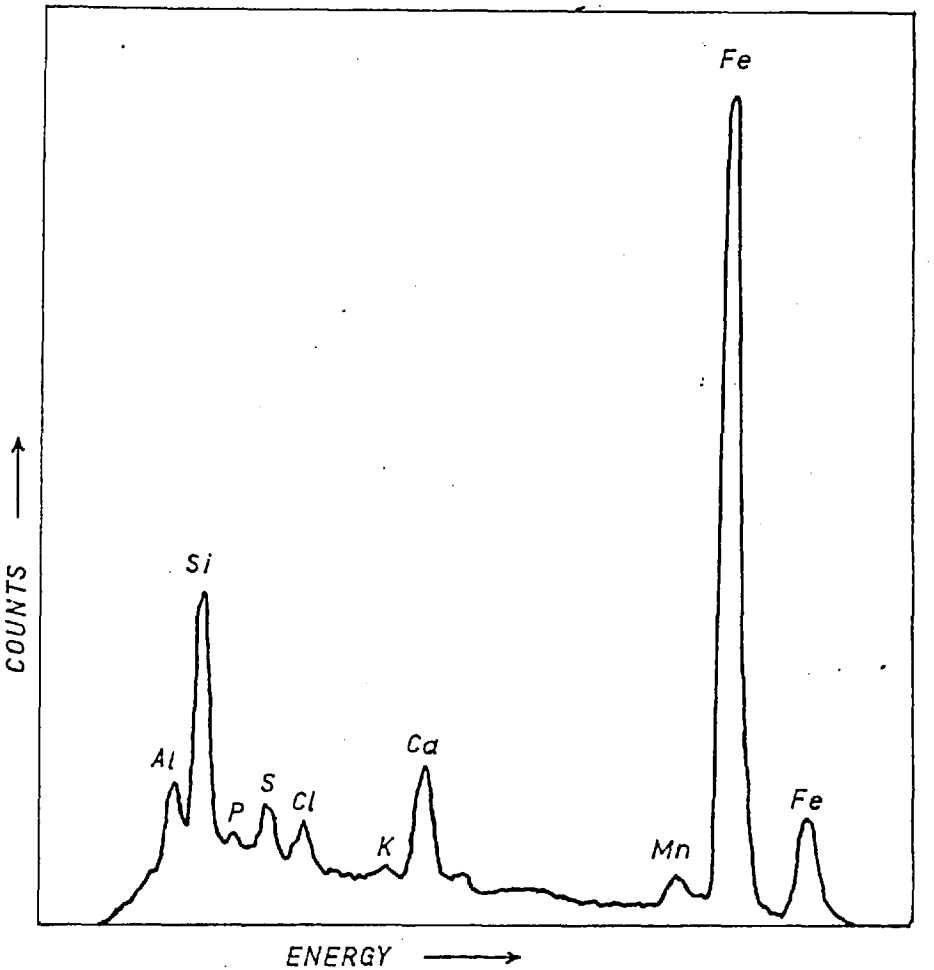
Fig. 99 shows two spectra resulting from a spot analysis of part of the sediment crust on an air dried Fagus leaf. It can clearly be seen that the analysis of the external surface (b) shows a large silicon peak as well as pronounced sulphur and chlorine peaks. By comparison, the analysis of the sediment encrustations originally in contact with the leaf surface (a), exhibits no silicon peak at all and the sulphur and chlorine peaks are considerably attenuated. The attenuation of sulphur and chlorine may be due to X-ray absorbtion by virtue of the fact that the analysis was, of necessity, restricted to a portion of the specimen not 'seen' directly by the detector. The loss of the silicon peak, however, is so complete that it is unlikely that such an effect could explain its absence. Rather, the analysis indicates that the sediment in contact with the leaf is almost entirely composed of iron rich material, most probably finely divided ferric oxide/hydroxide. This encrustation is seen to faithfully reproduce the surface features of the leaf and may well have been deposited as the result of the activity of microorganisms, although this is merely conjecture at the present time. After this deposit had formed on the leaf the coarser fractions of the sediment, namely the quartz grains and diatom frustules, became incorporated.

Fig. 103 shows the results of analyses carried out on Quercus,

Fig. 99.



(a) X-ray microanalysis spectrum of the sediment encrustation on a leaf: the surface of the encrustation in contact with the leaf.



(b) X-ray microanalysis spectrum of the external surface of the sediment encrustation on a leaf.

Betula and Salix leaves both freshly abscissed and after being in the stream or lake for 1 month. The freshly fallen leaves show reasonably consistent Pk/Bg ratios between replicates for some elements, but others fluctuate considerably. Of course there is no way of knowing if this fluctuation is real or not and analyses of adjacent areas on the same specimen occasionally show similar variations.

Quercus appears to contain more silicon than either Betula or Salix and this appears to be retained during exposure to the depositional environments, but the variation in the silicon Pk/Bg ratio is extremely large. In the freshly fallen leaves, Salix is outstanding in having high levels of calcium but this is found to become comparable with the other species after entry into the depositional environments. All species have potassium present when freshly fallen, but as one would expect it is rapidly leached. Iron increases dramatically in all species after deposition.

After only one month all species show similar elemental compositions in spite of considerable differences in the fresh state. No differences are discernible between either lake or stream deposited leaves.

Examination of Figs. 100-102, reveals that at least in Quercus and Salix there is no significant change in the elemental composition of the leaves during the first eight months in the stream and, in the case of Salix, the lake environment.

The leaves representing the four month sample were unfortunately not properly dried. This was due to a cracked 'O' ring plate on the freeze dryer which resulted in an air leak. Consequently, considerable redistribution of ions and tissue degradation took place. This is reflected in the Salix analysis (Fig. 100).

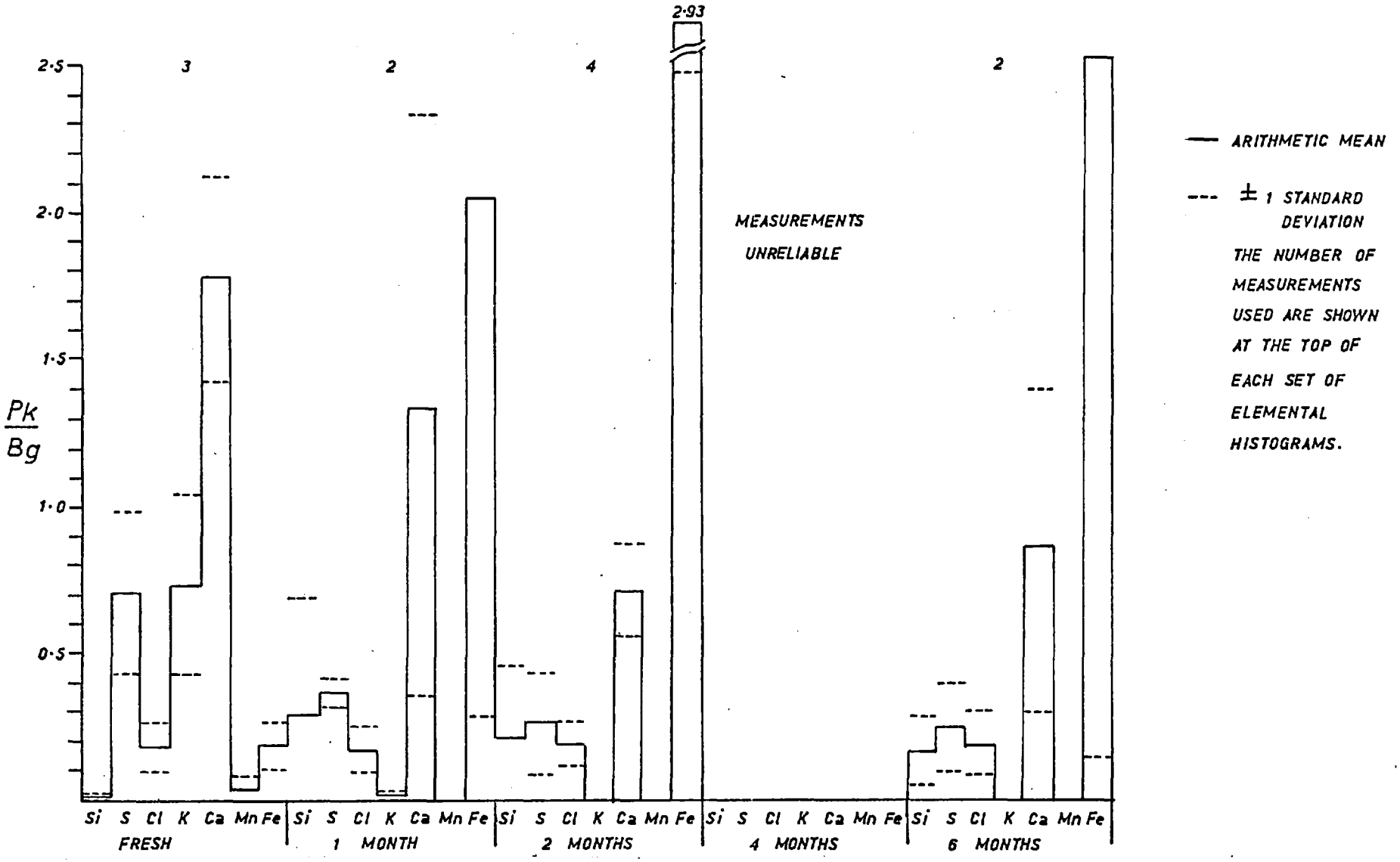


Fig. 100. Results of the X-ray microanalyses of Salix cinerea leaves showing changes in elemental composition during exposure to the stream environment.

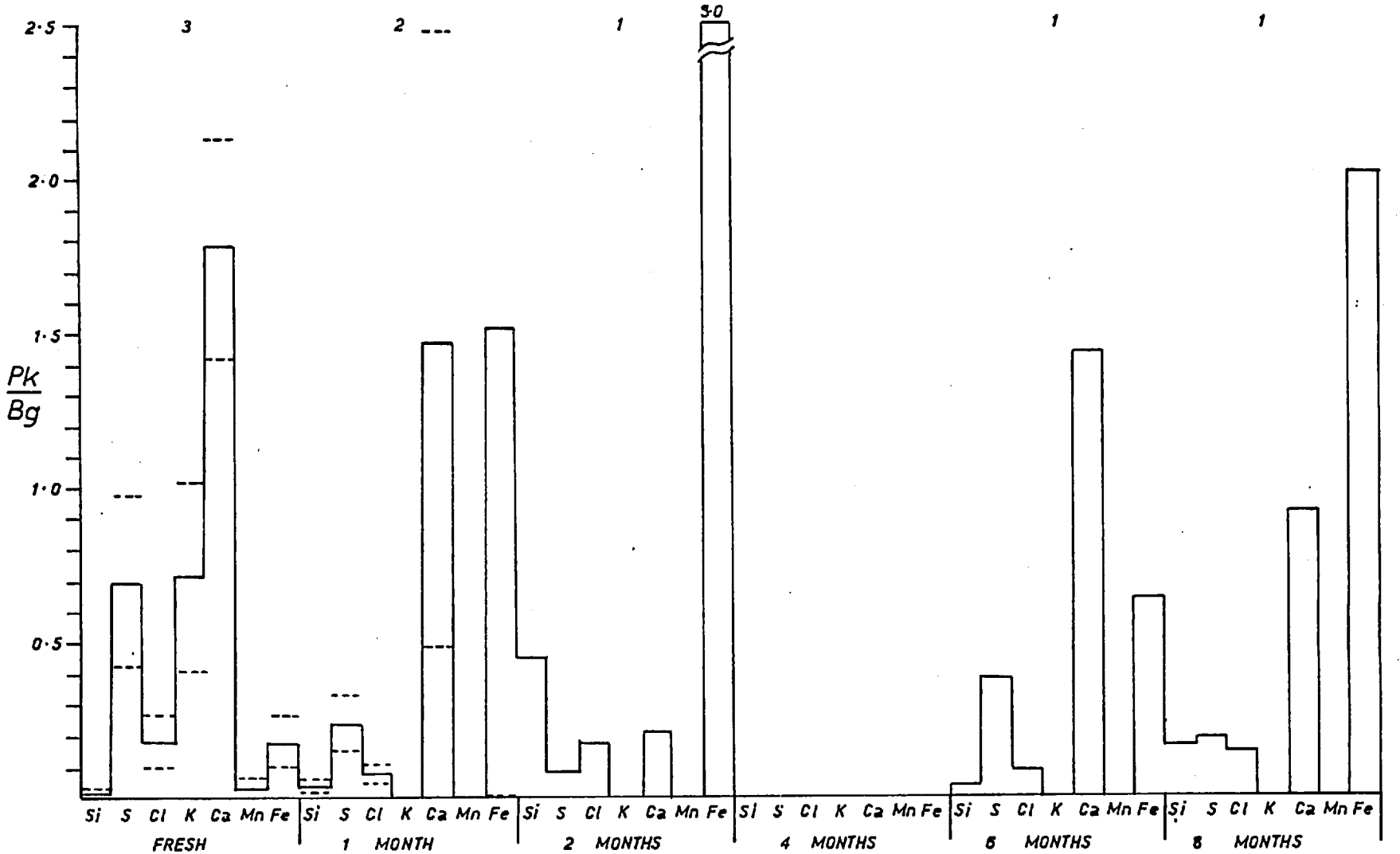


Fig. 101. Results of the X-ray microanalyses of Salix cinerea leaves showing changes in elemental composition during exposure to the lake bottom environment

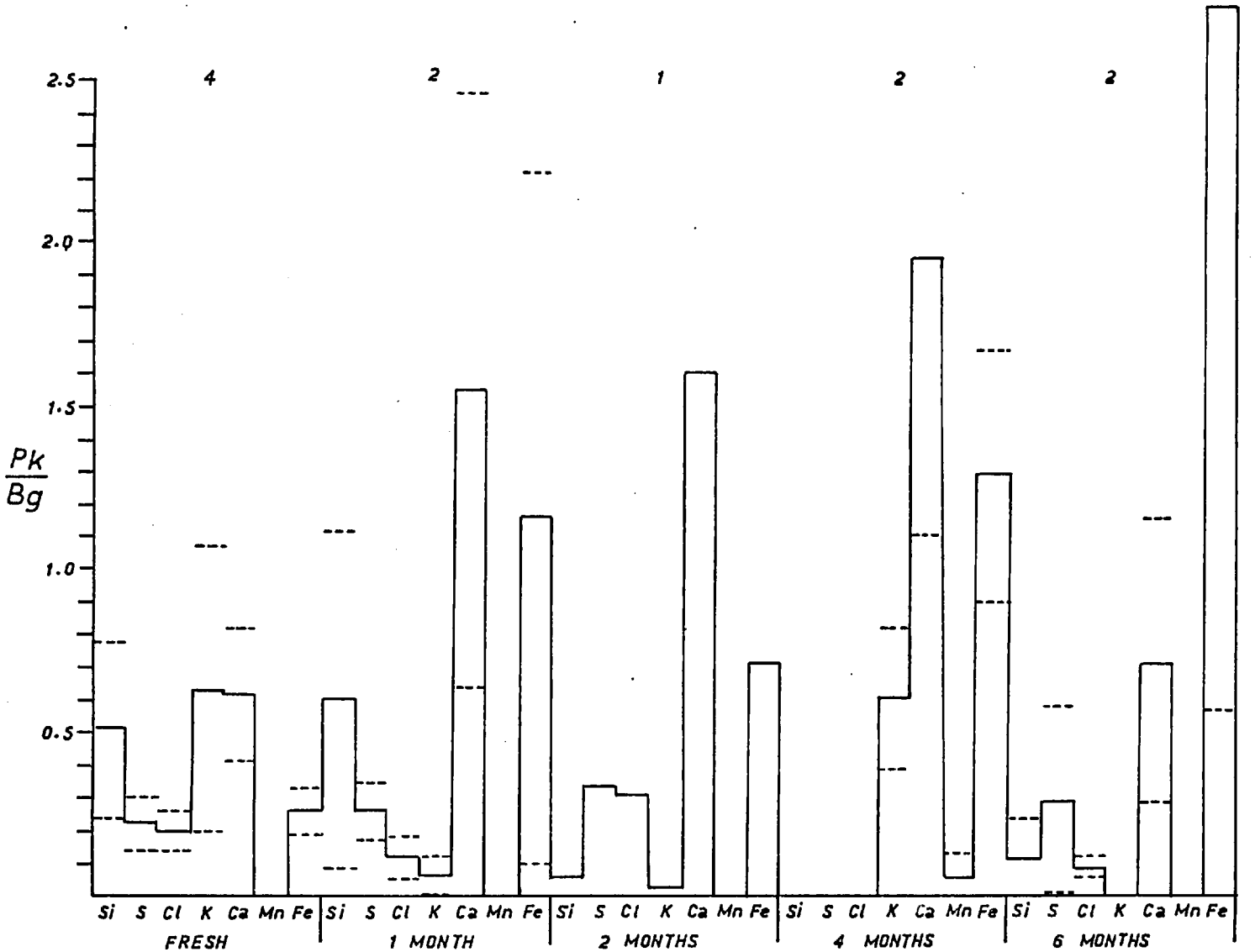
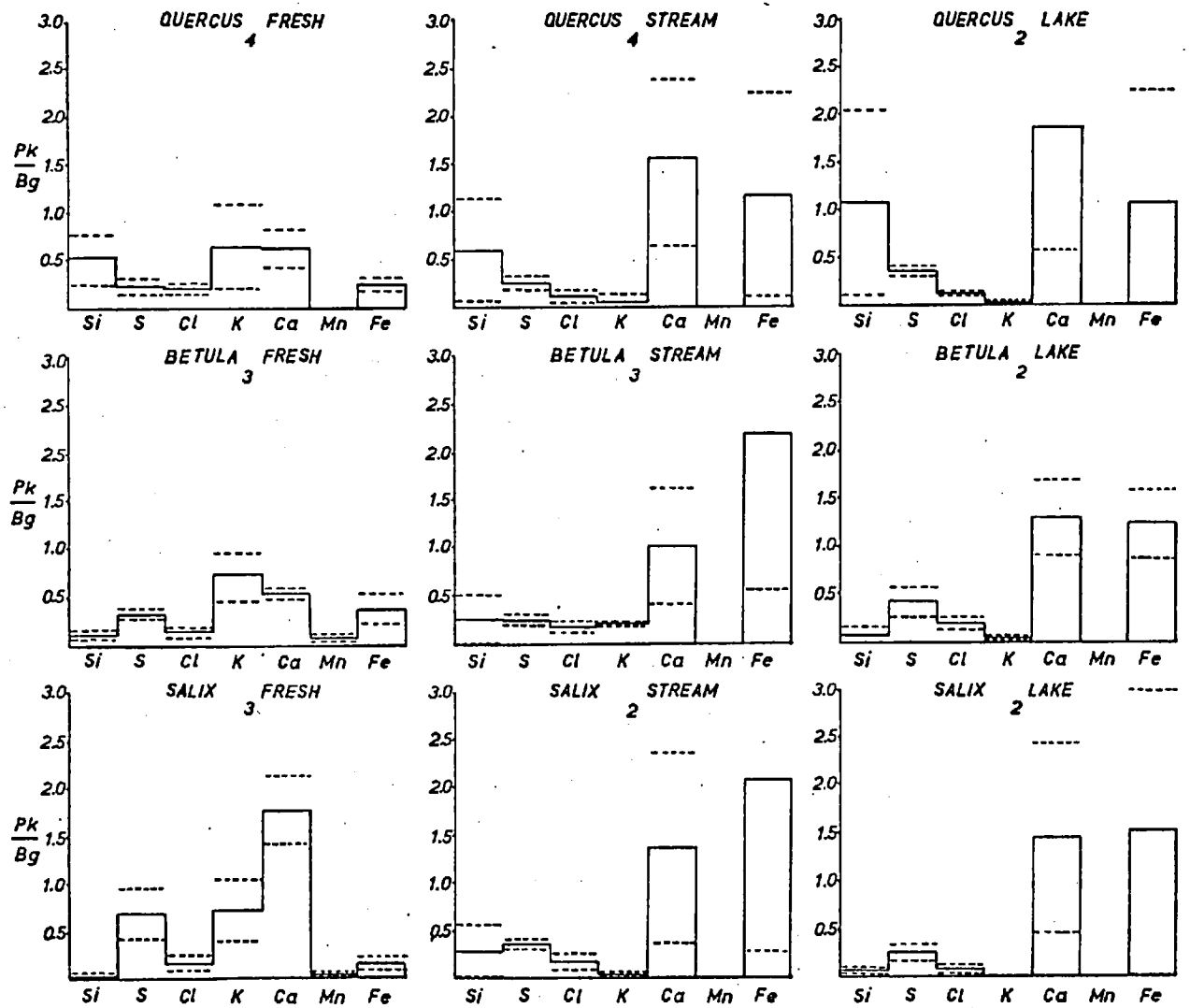


Fig. 102. Results of the X-ray microanalyses of Quercus leaves showing changes in the elemental composition during exposure to the stream environment.

Fig. 103. Histograms showing the elemental composition of Betula, Salix cinerea, and Quercus, both fresh and after 1 month exposure to the stream and lake environments. One standard deviation either side of the arithmetic mean (solid line) is shown by dotted lines. The number of samples in each treatment is given below the treatment heading.


QUERCUS FRESH 4
QUERCUS STREAM 4
QUERCUS LAKE 2
BETULA FRESH 3
BETULA STREAM 3
BETULA LAKE 2
SALIX FRESH 3
SALIX STREAM 2
SALIX LAKE 2
Pk/Bg
3.0
2.5
2.0
1.5
1.0
0.5
Si S Cl K Ca Mn Fe

Within the limits of the available information, one may therefore conclude that, although leaves may exhibit considerable differences in elemental composition when they are abscissed, they rapidly come into equilibrium with the entombing sediment and any differences in elemental composition are lost. No further changes were noted during the first eight months of deposition. Such observations are, however, limited due to the large variations exhibited even between replicates. It is unlikely that any variations in degradation rate are ascribable to the elemental composition of leaves, except perhaps for silicon which remains, when present as it is in the case of Quercus, within the leaf after deposition.

CONCLUSIONS

In order to investigate the large number of simultaneous processes that lead to the formation of a fossil plant deposit, a diverse and multidisciplinary approach had to be adopted. Obviously a restricted study of this kind cannot be definitive, but certain conclusions may be drawn, some of which may seem obvious on reflection, others not so. Much has been taken for granted in the past concerning the mechanisms of deposition and sorting, but if palaeobot ny is ever to gain from a more quantitative approach then these, often basic, assumptions must be tested.

It is clear from the results of the present study, and from a consideration of the number of variables involved, that it is unlikely that any direct relationships between the abundance of the component species of the source vegetation, and their representation in the fossil assemblage, will ever be found. The number of factors affecting litter production alone are sufficiently complex to introduce large fluctuations in the source material, which, when mechanisms of transport, deposition and diagenesis have disproportionately sorted the plant remains, produce such a wide range of possible abundances within the fossil deposit that direct interpretation becomes meaningless. The use of a closed system of expressing species proportions (e.g. percent scales) also means that the gross overrepresentation of stream and lakeside plants seriously biases the proportions of the other species. Even species which are clearly local to the depositional environment will be seriously under-represented if they are growing behind a screen of other vegetation.

The only way in which non streamside extra-local species can be represented, is by wind transport of their leaves to the depositional

environment. While laboratory experiments indicate that leaves with a low weight per unit area have a low settling velocity in still air and are easily blown along the ground, only those leaves exposed to high wind energies will be transported significant distances. For this reason extra local species are only represented by small 'sun' leaves. The significant size sorting that therefore occurs will invalidate any investigation that rests heavily on leaf size analysis.

Although proportional representation of the component species of the source vegetation is not to be expected, positional information may be preserved. By investigating the positions of plant remains within a deposit, with due regard to the mechanisms of deposition, associations of the source species within the original vegetation may be deduced. In order to do this the three dimensional nature of the deposit must be analysed, the depositional environment must be appreciated, and the relationship between the organic matter and the inorganic sediment determined. Because mechanical fragmentation occurs predominantly as a result of water transport, examination of the fragmentary condition of the fossil remains is also instructive. If an assemblage consists of both whole and fragmented leaves, then analysis of the distribution of these forms separately can provide valuable information on the species distributions within the source vegetation.

Fragmentation during water transport may be categorized according to the causal agency. The first major division is between fragmentation due to biological agencies and that caused by mechanical damage. Broadly speaking biological degradation, which can take place in both stream and lake bottom environments, may be divided into that produced by invertebrate detritivores, both large particle feeders and small particle feeders, and that caused by microorganisms. Mechanical degradation usually only occurs, in any great quantity, in fluviatile environments. By examining the type of degradation of the damaged

leaves, particularly within a deposit arising from the type of environment as that studied at Silwood, it should be possible, even in the absence of inorganic sedimentary structures, to distinguish those leaves which grew upstream from those growing locally.

From the cores taken through the Silwood delta it is evident that two leaf beds are formed and their separation is determined as a result of the hydrodynamic properties of leaves and sediment interacting with the fluid flow at the mouth of the stream. It is unlikely, however, that a theoretical approach to the elucidation of the fluid dynamic properties of leaves is likely to furnish information relevant to the interpretation of fossil deposits. An empirical approach might be more rewarding.

Any species distributions that might originally be present within a fossil deposit could well be seriously distorted by the immediate post depositional differential degradation of plant material. Thus, in the Silwood deposit we find an almost complete loss of the abundant local Alnus leaves from the lake bottom. It is only when deposition is abnormally rapid that such species are preserved. A general principal to be learned is that since preservation is evidently linked to speed of burial, as reflected in the consolidated rock by sediment type and sedimentary structures, analysis of fossil remains should include specimens from all parts of the deposit and not just the remains occurring within concentrated 'leaf beds'. Species abundance and type are likely to be closely linked with lithology, even though all the remains represent the same source vegetation.

Subsequent diagenetic changes, of course, further modify the assemblage, either leading to the preservation of destruction of species. X-ray microanalysis yielded large variations in leaf elemental composition, even between replicates, which meant that this technique

was of limited use in studying the trends of element exchange between the leaves and sediment during the first few months of burial. It was hoped that it would be possible to detect species differences in the exchange rates that could be linked to preservation, but this was not possible. However, the technique was useful in examining the distribution of silicon within the sediment encrustation that formed on the leaves, indicating that the fidelity of the leaf surface impression was due to the development, possibly of biogenic origin, of finely divided ferric oxide/hydroxide flocs. The early formation of such an encrustation undoubtedly aids in the preservation of the leaf, either by limiting microbial colonization of the tissues or by forming the basis for an impression fossil.

Post burial diagenetic changes are likely to be closely linked with the chemistry and porosity of the entombing matrix, and in this respect preservation is again strongly influenced by lithology. Hence it was not surprising that in the Hasty Bank study strong relationships between the various assemblages of plant remains and lithology were found. Another reason for the apparent lithological control was the use of density measures since, as has been discussed, density, being a measure of the number of depositional events of plant remains per unit volume of rock, is linked to the deposition processes of the matrix.

It is clear that when quantitatively sampling fossil plant deposits a large number of essentially lithological factors prevent the sampling regime from being what would be considered ideal. Therefore, robust statistical methods have to be used. The usefulness of the ability of both P.C.A. and R.A. to detect and display both trends and discontinuities within the data is self evident. However, these trends are only displayed when the data is appropriately treated to remove a lot of the 'random' variation which is such a characteristic of palaeontological

data.

Standardization of the data to zero mean and unit variance did not lead to any significant improvement of the ordinations of either Silwood or Hasty Bank data. However, the Hasty Bank ordinations were considerably clarified when the density data was logarithmically transformed. It appears that where high densities of fossil material are encountered, as at Hasty Bank, such a procedure is useful. Of more practical significance is the use of a pseudo log density abundance scale that can be assessed visually in field conditions. The successful adoption of such a technique is demonstrated in the Hasty Bank ordinations.

To say one statistical method is correct under a particular set of circumstances, and others are not is, of course, erroneous in itself since there is no absolute with which to compare. Therefore, one has to decide on a method which ordinates the data in a way that can be most readily interpreted in the light of theoretical expectations and practical experience. In this respect analyses of the data from both Silwood and Hasty Bank was more meaningfully presented by Reciprocal Averaging.

R.A. is an ordination technique that, by comparison with principal components analysis, offers a number of advantages for the investigation of the distribution of fossil macroremains. The duality of the stand and species plots makes it a technique particularly useful for detecting the relationship between assemblage structure and lithology, while another important characteristic is that the R.A. ordinations are not affected by overall species abundance, as P.C.A. apparently is. There can be no doubt that future investigations will confirm R.A. as an extremely powerful palaeoecological tool.

Such work as has been carried out here represents an investigation of only a single depositional environment, and consequently the extrapolation of the findings to situations other than a fluvio lacustrine delta system is extremely dubious. However, attempts have been made to generalize where possible, and by studying a number of aspects, in what is after all, a multivariate system, it has been possible to assess the relative importance of the factors which determine the structure of a fossil plant deposit. However, deposition in the Silwood situation has been gradual and progressive, and periods of abnormal conditions have been brief. It is probable that many of the more important depositional events are the result of local 'catastrophies' such as flood conditions following a storm. Here rapid burial will ensure a large, and perhaps, more representative sample of the source vegetation will be preserved. Observations of such events are desperately needed, as are investigations of deposits resulting from such abnormal, although in geological terms frequent, events.

The use of multivariate ordination techniques has been demonstrated here and shown to be successful in detecting patterns of distributed plant remains within deposits. Although 'robust' techniques, they do have a theoretical requirement that the data should be multivariate normally distributed. Further advances may be made by the use of the so called 'distribution free' techniques such as those based on information theory. Under these circumstances the source vegetation may be thought of as a message source, the deposition and fossilization processes as the channel, and the sampling of a fossil assemblage, the receiver in an information transmission system. The use of information theory in phytosociological studies has already been

investigated by Orlóci (1968), and in the analysis of pollen diagrams by Dale and Walker (1970). Similar approaches to the analysis of the distributions of plant remains within fossil deposits may well prove profitable.

APPENDIX

APPENDIX TABLE 1 Fragment Density per Quadrat Silwood Delta Samples

STAND	ALNUS	BETULA	FAGUS	QUERC.	SALIX C	ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
1	1	7	0	0	4	0	0	0	0	0	7	0
2	5	0	0	1	0	2	0	0	0	0	0	0
3	6	4	1	0	1	0	0	0	0	0	0	0
4	9	2	1	3	3	0	4	0	0	0	0	0
5	14	4	1	1	6	2	0	0	1	1	0	0
6	18	0	7	5	2	0	2	1	0	1	0	0
7	17	2	0	1	6	3	2	1	0	1	0	0
8	23	3	6	2	2	0	0	0	0	9	0	0
9	22	4	3	4	6	1	2	0	0	4	0	0
10	25	5	0	2	5	3	0	0	0	5	0	0
11	30	2	0	4	2	0	0	0	0	5	0	0
12	34	7	0	3	4	3	0	0	0	6	0	0
13	36	6	2	7	4	1	0	0	0	3	0	0
14	42	4	0	1	4	1	0	0	0	2	0	0
15	41	2	0	4	4	0	0	0	0	1	0	0
16	44	2	0	2	3	0	0	0	0	1	0	0
17	42	1	0	2	1	0	0	0	0	0	0	0
18	43	3	0	0	3	0	0	0	0	1	0	0
19	45	4	0	2	1	0	0	0	0	1	0	0
20	47	6	0	2	0	0	0	0	0	1	0	0
21	48	7	0	2	0	0	0	0	0	1	0	0
22	49	11	0	2	0	0	0	0	0	1	0	0
23	50	14	0	2	0	0	0	0	0	1	0	0
24	51	5	0	2	0	0	0	0	0	1	0	0
25	52	9	0	2	0	0	0	0	0	1	0	0
26	53	5	0	2	0	0	0	0	0	1	0	0
27	54	6	0	2	0	0	0	0	0	1	0	0
28	55	10	0	2	0	0	0	0	0	1	0	0
29	56	6	0	2	0	0	0	0	0	1	0	0
30	57	3	0	2	0	0	0	0	0	1	0	0
31	58	2	0	2	0	0	0	0	0	1	0	0
32	59	1	0	2	0	0	0	0	0	1	0	0
33	60	1	0	2	0	0	0	0	0	1	0	0
34	61	0	0	2	0	0	0	0	0	1	0	0
35	62	0	0	2	0	0	0	0	0	1	0	0
36	63	0	0	2	0	0	0	0	0	1	0	0
37	64	0	0	2	0	0	0	0	0	1	0	0
38	65	0	0	2	0	0	0	0	0	1	0	0
39	66	0	0	2	0	0	0	0	0	1	0	0

APPENDIX TABLE 1 (CONT.)

STAND	ALNUS	BETULA	FAGUS	QUERC.	SALIX C	ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
40	3	0	0	1	0	0	0	0	0	0	0	0
41	31	1	3	59	55	8	1	0	0	0	0	0
42	28	0	0	16	6	6	0	0	0	0	0	0
43	13	0	7	17	3	4	0	0	0	0	0	0
44	6	0	5	2	5	3	0	0	0	0	0	0
45	7	0	0	4	2	2	0	0	0	0	0	0
46	8	0	6	1	1	1	0	0	0	0	0	0
47	30	0	1	14	6	3	0	0	0	0	0	0
48	8	0	0	5	4	0	0	0	0	0	0	0
49	22	1	1	3	1	1	0	0	0	0	0	0
50	21	1	2	3	1	0	0	0	0	0	0	0
51	11	0	0	1	0	0	0	0	0	0	0	0
52	2	0	0	0	0	0	0	0	0	0	0	0
53	21	0	0	2	1	0	0	0	0	0	0	0
54	11	0	0	0	1	0	0	0	0	0	0	0
55	3	1	5	10	5	1	0	0	0	0	0	0
56	15	0	1	17	1	0	0	0	0	0	0	0
57	11	0	0	16	2	0	0	0	0	0	0	0
58	12	0	0	5	2	0	0	0	0	0	0	0
59	4	0	0	2	1	0	0	0	0	0	0	0
60	2	0	0	1	0	0	0	0	0	0	0	0
61	10	0	3	3	2	1	0	0	0	0	0	0
62	1	0	0	1	0	0	0	0	0	0	0	0
63	4	0	1	3	1	0	0	0	0	0	0	0
64	14	0	3	6	2	1	0	0	0	0	0	0
65	12	0	0	1	0	0	0	0	0	0	0	0
66	12	0	0	0	0	0	0	0	0	0	0	0
67	2	0	0	0	0	0	0	0	0	0	0	0
68	10	0	0	0	0	0	0	0	0	0	0	0
69	4	0	0	0	0	0	0	0	0	0	0	0
70	1	0	0	0	0	0	0	0	0	0	0	0
71	2	0	0	0	0	0	0	0	0	0	0	0
72	4	0	0	0	0	0	0	0	0	0	0	0
73	4	0	0	0	0	0	0	0	0	0	0	0
74	1	0	0	1	0	0	0	0	0	0	0	0
75	9	0	0	0	0	0	0	0	0	0	0	0
76	39	1	1	1	1	0	0	0	0	0	0	0
77	4	0	0	0	0	0	0	0	0	0	0	0
78	5	0	0	0	0	0	0	0	0	0	0	0
79	7	0	3	2	6	0	0	1	0	0	0	0

APPENDIX TABLE 2 Whole Leaf Density per Quadrat

STAND	ALNUS	BETULA	FAGUS	QUERC.	SALIX C	ILEX	AESC.	ACER	CRIT.	TYPHA	NUPHAR	SALIX A
1	39	31	22	4	52	0	1	0	0	0	0	0
2	4	3	5	1	7	0	1	0	0	0	0	0
3	6	1	0	0	1	0	0	0	0	0	0	0
4	4	2	14	0	5	0	0	0	0	0	0	0
5	9	0	1	0	2	0	0	0	0	0	0	0
6	11	1	2	1	5	0	0	0	0	0	0	0
7	11	0	0	1	4	0	1	0	0	0	0	0
8	12	1	9	1	26	0	0	0	0	0	0	0
9	8	0	3	2	6	0	0	0	0	0	0	0
10	7	1	1	4	24	0	0	0	0	0	0	0
11	7	2	0	3	5	0	0	0	0	0	0	0
12	2	4	1	3	11	0	0	0	0	0	0	0
13	7	5	1	1	4	0	0	0	0	0	0	0
14	3	3	1	3	6	0	0	0	0	0	0	0
15	5	1	1	7	3	0	0	0	0	0	0	0
16	7	2	0	1	0	0	0	0	0	0	0	0
17	16	7	10	1	12	0	2	0	0	0	0	0
18	3	1	6	0	3	0	0	0	0	0	0	0
19	4	1	3	0	1	0	0	0	0	0	0	0
20	1	1	16	4	1	0	0	0	0	0	0	0
21	1	1	0	1	1	0	0	0	0	0	0	0
22	2	1	4	1	1	0	0	0	0	0	0	0
23	4	1	3	0	3	0	0	0	0	0	0	0
24	5	1	2	2	2	0	0	0	0	0	0	0
25	6	4	0	0	3	0	0	0	0	0	0	0
26	6	2	0	6	6	0	0	0	0	0	0	0
27	4	1	0	1	2	0	0	0	0	0	0	0
28	6	2	0	1	1	0	0	0	0	0	0	0
29	5	1	0	1	1	0	0	0	0	0	0	0
30	11	5	0	1	11	0	0	0	0	0	0	0
31	6	1	0	0	2	0	0	0	0	0	0	0
32	6	1	0	0	1	0	0	0	0	0	0	0
33	6	1	0	0	1	0	0	0	0	0	0	0
34	6	1	0	0	1	0	0	0	0	0	0	0
35	6	1	0	0	1	0	0	0	0	0	0	0
36	6	1	0	0	1	0	0	0	0	0	0	0
37	6	1	0	0	1	0	0	0	0	0	0	0
38	12	1	7	2	2	0	0	0	0	0	0	0
39	3	1	7	2	2	0	0	0	0	0	0	0

APPENDIX TABLE 2 (CONT.)

STAND	ALNUS	BETULA	FAGUS	QUERC.	SALIX C	ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
4	0	2	1	0	0	0	0	0	0	0	0	0
4	1	0	5	0	27	0	0	0	0	0	0	0
4	2	1	0	0	3	0	0	0	0	0	0	0
4	3	4	3	0	1	0	0	0	0	0	0	0	0
4	4	2	0	0	1	0	0	0	0	0	0	0
4	5	1	2	0	3	0	0	0	0	0	0	0
4	6	1	0	0	3	0	0	0	0	0	0	0
4	7	1	0	0	4	0	0	0	0	0	0	0
4	8	1	0	0	1	0	0	0	0	0	0	0
4	9	1	0	0	1	0	0	0	0	0	0	0
5	0	1	0	0	1	0	0	0	0	0	0	0
5	1	2	0	0	1	0	0	0	0	0	0	0
5	2	3	0	0	1	0	0	0	0	0	0	0
5	3	4	0	0	1	0	0	0	0	0	0	0
5	4	5	0	0	1	0	0	0	0	0	0	0
5	5	6	0	0	1	0	0	0	0	0	0	0
5	6	7	0	0	1	0	0	0	0	0	0	0
5	7	8	0	0	1	0	0	0	0	0	0	0
5	8	9	0	0	1	0	0	0	0	0	0	0
5	9	1	0	0	1	0	0	0	0	0	0	0
6	0	1	0	0	1	0	0	0	0	0	0	0
6	1	2	0	0	1	0	0	0	0	0	0	0
6	2	3	0	0	1	0	0	0	0	0	0	0
6	3	4	0	0	1	0	0	0	0	0	0	0
6	4	5	0	0	1	0	0	0	0	0	0	0
6	5	6	0	0	1	0	0	0	0	0	0	0
6	6	7	0	0	1	0	0	0	0	0	0	0
6	7	8	0	0	1	0	0	0	0	0	0	0
6	8	9	0	0	1	0	0	0	0	0	0	0
6	9	1	0	0	1	0	0	0	0	0	0	0
7	0	1	0	0	1	0	0	0	0	0	0	0
7	1	2	0	0	1	0	0	0	0	0	0	0
7	2	3	0	0	1	0	0	0	0	0	0	0
7	3	4	0	0	1	0	0	0	0	0	0	0
7	4	5	0	0	1	0	0	0	0	0	0	0
7	5	6	0	0	1	0	0	0	0	0	0	0
7	6	7	0	0	1	0	0	0	0	0	0	0
7	7	8	0	0	1	0	0	0	0	0	0	0
7	8	9	0	0	1	0	0	0	0	0	0	0
7	9	1	0	0	1	0	0	0	0	0	0	0

APPENDIX TABLE 3 Fragment Areas per Quadrat (cm^2)

STAND	ALNUS	BETULA	FAGUS	QUERC.	SALIX	C ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
1	[illegible]	22.5			5.0						185.0	
2	[illegible]	3.5		0.5		2.5						
3	[illegible]				0.5							
4	[illegible]	4.5	13.5	[illegible]	2.0		15.0				1.0	
5	92.5	1.0	[illegible]	1.0	17.5	2.0			0.5	0.5		
6	91.0	0.5	36.0	36.0	20.0	20.5		1.0		1.0		
7	116.5		24.5	42.0	23.0	4.5	2.5	1.0		0.5		
8	299.[illegible]	20.0	88.5	77.[illegible]	48.5	14.0	4.5	0.5	3.0	19.5		
9	161.[illegible]	6.5	0.0	4.[illegible]	6.[illegible]	1.[illegible]				51.[illegible]		
10	628.0	[illegible]		4.[illegible]	51.0	7.5	3.0		3.5	36.0		
11	173.5	24.5		5.5	[illegible]	3.[illegible]				17.[illegible]		
12	[illegible]	[illegible]		3.5	7.5		1.5			4.[illegible]		
13	614.[illegible]	32.[illegible]	1.5	21.[illegible]	41.[illegible]	4.0				19.0		20.5
14	[illegible]	12.[illegible]		0.5	24.0	1.5		1.0		17.5		5.5
15	42.[illegible]	[illegible]		32.5	3.0	1.5				2.5		
16	215.5	5[illegible]		11.5	4.[illegible]					3.5		28.5
17	43.[illegible]	10.5	49.5		+.[illegible]		49.5			3.0	4.5	
18	[illegible]	[illegible]									2.5	
19	[illegible]	2.[illegible]			0.5							
20	97.5			3.0		3.0	54.0			2.5	1.5	
21	144.[illegible]		6.5	[illegible]	12.[illegible]	3.0				2.[illegible]	1.0	
22	4[illegible]	1.5	[illegible]	[illegible]	11.[illegible]	5.[illegible]	7.5		1.5		[illegible]	
23	214.5		28.[illegible]	31.[illegible]	7.[illegible]	3.5					7.5	
24	2[illegible]	1.5	23.5		5.[illegible]	3.0					21.5	
25	[illegible]	2.[illegible]	27.[illegible]	56.5	14.[illegible]	22.[illegible]				4.0		
26	22.5	[illegible]	17.0		7.5	7.5				1.5		
27	448.5	45.[illegible]	5.[illegible]	42.5	91.[illegible]	5.[illegible]	1.5			18.5		18.5
28	56.[illegible]				[illegible]					2.5		
29	60.5	4.5	[illegible]	2.[illegible]	15.[illegible]							
30	40.5		[illegible]	1.5	4.5	1.0				1.5		
31	[illegible]	16.[illegible]		[illegible]	[illegible]					5.5		
32	118.5	11.[illegible]	9.[illegible]	22.[illegible]	3.[illegible]	5.0				4.[illegible]		
33	[illegible]	13.[illegible]	19.[illegible]	2.[illegible]	42.5	3.5				5.[illegible]	0.5	5.0
34	[illegible]	[illegible]								14.5		4.0
35	17.[illegible]			[illegible]	2.[illegible]	1.5				3.5		
36	167.5	11.[illegible]		1.[illegible]	8.0	2.0				2.[illegible]		
37	75.[illegible]			[illegible]							1.0	
38	61.[illegible]	6.[illegible]		[illegible]	0.5					3.[illegible]		
39	45.5	1.[illegible]	1.5	4.5	3.0		44.5					

APPENDIX TABLE 3 (CONT.)

STAND	ALNUS	BETULA	FAGUS	QUER.	SALIX	C ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
40	21.5			4.5								
41	66.5	12.5	72.5	70.5	98.5	4.5		0.5	0.5			
42	37.5		13.5	18.5	2.5	7.5						
43	21.5		12.5		22.5	3.5	1.5			1.5		1.5
44	17.5	11.5		4.5	6.5					2.5		
45	15.5	22.5	14.5	23.5	13.5	4.5				13.5		
46	21.5	6.5			2.5	1.5				1.5		
47	1.5	18.5	74.5	6.5	6.5	1.5				2.5		
48	22.5	12.5			10.5	1.5				1.5		
49	21.5				3.5	2.5				1.5		
50	22.5	14.5	6.5	2.5	1.5							
51	22.5	5.5	1.5	4.5	20.5	10.5				5.5	1.5	
52		16.5		1.5	6.5					1.5		
53	15.5	12.5				3.5				5.5		
54	74.5	14.5			6.5					5.5	2.5	
55	4.5	1.5		1.5	2.5					6.5		
56	75.5		57.5	98.5	95.5	3.5			1.5			2.5
57	26.5	3.5	6.5	2.5	6.5	4.5						
58	56.5	6.5	1.5	26.5	6.5		27.5					
59	22.5	6.5	61.5	65.5	7.5	3.5				5.5	1.5	
60	16.5		1.5	3.5	1.5					6.5		
61	54.5	2.5	1.5	1.5	2.5	3.5				2.5		
62	99.5	2.5	1.5	1.5	6.5							
63	43.5	1.5										
64	6.5			4.5	1.5	0.5						
65	12.5	9.5	1.5	4.5	9.5							
66	12.5			19.5	3.5	3.5					6.5	
67	42.5	9.5		1.5	8.5							
68	31.5				1.5							
69	11.5	6.5			1.5	0.5				13.5		
70	44.5	6.5	4.5	3.5	2.5	1.5				5.5		
71	23.5			2.5	9.5	6.5				1.5		
72	1.5		1.5		6.5	1.5		5.0				
73			1.5			1.5						
74	27.5	7.5	14.5	16.5	9.5	3.5						
75			1.5	2.5								
76	15.5	2.5	24.5	10.5	14.5	9.5	21.5			1.5		
77	38.5				2.5	1.5				5.5		
78		7.5		1.5	4.5							
79	6.5	4.5	2.5	12.5	6.5	2.5		1.5				

APPENDIX TABLE 4 Total Area of Whole Leaves per Quadrat (cm^2)

STAND	ALNUS	BETULA	FAGUS	QUERC.	SALIX	C ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
1	564.0	19	216.5	62.	2		124.5					
2	37.	5.	58.0	34.0	11.5		53.5					
3	70.	6.			6.		53.0					
4	30.5	9.0	167.		12.5							
5	134.		8.5		3.5							
6	183.	7.5	42.	13.5	23.5							
7	180.	2.5			26.5		2.5					
8	462.	83.5	131.5	7.	155.		5.0					
9	415.5			39.5	15.5							9.0
10	13421	54.	5.5	49.	97.	6.5			3.5			31.5
11	331.	16.		20.	43.							
12	554.	134.		10.	125.				2.5			16.0
13	263.	46.	7.	68.	31.5							
14	634.	29.5	7.5	46.0	3.5	9.0						
15	86.5	111.		139.	27.5							53.0
16	820.	59.5			13.5				1.0			
17	250.	7.5	121.	6.0	33.5		71.0					
18	25.5	6.5	76.5			1.5						
19	58.5		37.5		12.							
20	14.	1.	179.									
21	2.	6.0			15.5							
22	5.		14.5	2.0	1.5							
23	9.		57.5		10.							
24	32.	3.5			1.							
25	199.	21.5	39.5	22.0	135.	11.0						
26	22.	15.	23.0		55.5				8.0			
27	638.5	21.5		77.0	128.							
28	12.				16.							
29	21.5	2.		4.5	5.							
30	34.	2.		15.	15.	2.5						
31	96.5	6.		51.5	47.							
32	172.5	4.			12.							
33	4.	22.		28.	39.5							11.5
34	309.5	5.	25.5									19.5
35	267.	14.			0.5							
36	75.	5.5			2.5							
37	110.	40.			7.5							
38	65.	10.										
39	46.5		91.5	18.5	7.5							

APPENDIX TABLE 4 (CONT.)

STAND	ALNUS	BETULA	FAGUS	QUERC.	SALIX C	ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
40			12.0									
41	86.5	16.5	45.5	44.5	170.0							
42					12.0							
43			19.0		6.5							1.5
44		4.5		20.5	9.5							
45	241.5	2.0	144.5	25.5	1.5							
46	6.5		17.5									
47	12.0	31.0	50.0		17.5							
48	11.5	16.5		14.5	5.5							
49	23.5	8.5			12.5							
50	39.5	17.5		4.5	7.0							
51	64.5		17.5		8.5							
52	76.5	16.5			8.5							
53	57.5	43.5		75.5								
54	19.0	1.0	39.5		2.0							
55					1.0							
56	53.0		44.0	39.5	46.5							
57	36.0	3.5	37.5									
58	26.5		47.0	4.0	10.5							1.5
59		6.0	4.5									
60			27.5		4.5							
61	17.5	11.0	32.0		7.0							
62		6.0			4.5							
63			15.0									
64	2.0				8.0							
65	32.5	12.5			9.0							
66					4.5							
67	58.0	18.5										
68	44.0											
69	1.5				1.0							
70	26.5				7.5							
71		1.5			0.5							
72	3.5	6.5										
73			15.5	29.0								
74		3.0			0.5							
75	116.0	3.5	46.0		25.0		13.5					
76	251.0	12.5	212.5	23.0	32.5		39.5					
77			4.5	61.5	13.5							
78					0.5							
79		12.5	31.0		3.5							

APPENDIX TABLE 5 Area of all Leaf Material per Quadrat (cm^2)

STAND	ALNUS	BETULA	FAGUS	QUERC.	SALIX C	ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
1	594.5	212.5	216.5	62.0	213.5	0.0	124.5				185.0	
2	65.0	8.5	58.0	34.5	11.5	2.5	53.5					
3	138.5	6.0	1.0		6.5		53.0					
4	60.5	12.5	18.5	3.0	14.5		15.0				1.0	
5	226.5	1.0	10.5	1.0	26.0	2.0			0.5	0.5		
6	274.5	11.0	30.0	51.5	48.5	20.5		1.0		1.0		
7	290.5	3.5	24.5	42.0	49.5	4.5	5.0	1.0		0.5		
8	761.0	103.5	220.0	84.0	203.5	14.0	6.5	0.5	3.0	19.5		
9	576.5	6.5	8.0	42.5	21.5	1.0				51.0		9.0
10	1970.	197.0	5.5	53.0	148.0	14.0	3.0		7.0	36.0		31.5
11	505.0	41.0		25.5	91.0	3.0				13.0		
12	343.5	65.0	7.0	71.5	38.5	4.0	1.5			4.0		
13	1568.	166.	1.5	31.	166.5	4.0			2.5	19.0		36.5
14	985.0	41.0	7.5	46.5	33.5	10.5		1.0		17.5		
15	1330.	14.5		171.5	38.5	1.5				2.5		53.0
16	1035.	110.0	11.5	11.5	22.5				1.0	3.5		28.5
17	302.0	21.0	170.5	6.0	37.5		120.5			3.0	4.5	
18	34.5	0.5	76.5			1.5					2.5	
19	97.5	2.0	37.5		12.5							
20	111.5			3.0		3.0	54.0			2.5	1.5	
21	146.0	6.0	6.5	9.0	27.5	8.0				2.0	1.0	
22	46.0	0.5	48.0	10.5	12.5	5.0	7.5		1.5		0.5	
23	229.0		91.5	31.0	17.0	3.5					7.5	
24	405.5	22.5	65.5	78.5	149.0	33.0				4.0		
25	54.0	5.0	23.5		6.0	3.0					21.5	
26	114.5	17.0	40.0		68.0	7.5			8.0	1.5		
27	1687.	66.5	5.0	119.5	219.0	5.0	1.5			18.5		18.5
28	78.0				17.0					2.5		
29	62.0	6.5	0.5	6.5	20.0							
30	74.5	2.0	0.5	16.5	43.5	3.5				1.5		
31	204.5	24.0		51.0	55.5					5.5		
32	291.0	15.0	9.0	22.0	115.0	5.0				4.0		
33	578.5	0.5	10.0	39.0	82.0	4.5				5.0	0.5	16.5
34	576.0	5.0	25.5							14.5		23.5
35	437.5	12.5		0.5	7.0	1.5				7.5		
36	212.5	25.0		1.0	10.5	2.0				3.0		
37	140.0	40.0		2.0	7.5					3.0	1.0	
38	176.0	10.0		0.5	0.5					3.0		
39	92.0	1.0	93.0	4.5	3.0		44.5					

APPENDIX TABLE 5 (CONT.)

STAND	ALNUS	BETULA	FAGUS	QUERCUS	SALIX C	ILEX	AESC.	ACER	CRAT.	TYPHA	NUPHAR	SALIX A
40	21.0		12.0	4.0								
41	154.0	26.0	123.5	86.0	268.5	8.5	0.5		0.5			
42	27.0	6.0	13.5	16.5	14.0	7.5						1.5
43			19.0									
44				20.	9.5							
45	436.5	42.	158.	48.	6.	4.5				14.5		
46	27.5		26.		1.5	1.5				1.		
47	121.	49.	124.5		23.	1.0				2.		
48		25.		19.	16.	1.5				1.		
49	1	14.		3.	16.	2.0				1.5		
50	6	27.	0.5	7.	8.5							
51	15	5	19.0	4.	1.	10.0				6.0	1.0	
52	7	35.		1.	9.					1.		
53	7	46.		75.		0.5				5.		
54	9	15.	39.5		2.5					5.5	0.5	
55	4	1.		1.5	3.					0.5		
56	12		97.0	13	144	3.5			1.0			2.5
57	6	6.5	43.	2.		4.0						
58		4.	57.		17.		27.5					1.5
59	2	12.5	55.		7.	3.0				5.5	1.0	
60	16		22.	2.	6.					0.5		
61	71	27.	38.	3.		3.0				2.0		
62	9	8.	8.	1.	10.5							
63	43	6.	16.									
64	3		2.	3.	9.5	0.5						
65	45	22.	1.	4.	18.							
66	12			19.5	7.5	0.5					6.0	
67	142	27.5		1.	8.							
68	75				1.							
69	12		2.		2.5					18.5		
70	26		5	3.	1.	1.				5.		
71	23	7.		20.	9.	1.				1.		
72	3							5.0				
73			17.	37.								
74	27.	10.	14.	16.								
75	4			2.	25.	3.	13.5					
76	437	38.	237.	3.	47.	3.	61.0			1.0		
77	22		12.	54.	15.	1.5				5.0		
78	8.	7.		1.	4.							
79	6.5	16.5	32.	12.	8.	2.5						

Listed below is the FORTRAN IV Reciprocal Averaging program used in this thesis.

```
      PROGRAM RECAV(INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT,TAPE62)
      COMMON/A/IROW(100,3),ICOLA(100,3),M,N
      COMMON/B/ITITLE(8)
      COMMON/C/XA(100),Y(100),IZ(100),IALPHA(26)
      DIMENSION X(65,70),R(65),COLA(65),COLB(65),ROW(70),XX(65,2),Z(65,
     12),RZ(65,2),SXY(2),SXZ(2),F(2),SRZ(2)
      WRITE(6,7)
    7 FORMAT(1H1,50X,*RECIPROCAL AVERAGING*)
      READ(5,1)ITITLE
    1 FORMAT(8A10)
      WRITE(6,2)ITITLE
    2 FORMAT(1X,8A10)
      WRITE(6,38)
   38 FORMAT(/* F I R S T  A X I S*)
      LOOP=1
      READ(5,3)M,N
    3 FORMAT(2I3)
      DO 4 J=1,N
    4 READ(5,5)(X(I,J),I=1,M)
    5 FORMAT(20F4.0/20F4.0/17F4.0/)
      DO 6 I=1,M
    6 R(I)=0.
      DO 8 I=1,M
      DO 8 J=1,N
    8 R(I)=R(I)+X(I,J)
      SR=0.
      DO 9 I=1,M
      SR=SR+R(I)
      COLB(I)=0.
    9 COLA(I)=0.
      M1=M/2
      DO14I=1,M1
      II=RANF(0.)*FLOAT(M)+1.
   14 COLA(II)=100.
   31 IT=0
      IF(LOOP.GT.1.AND.IT.EQ.0)GOTO41
   21 IT=IT+1
      IRED=1
      DO 11 J=1,N
      ROW(J)=0.
      RN=0.
      DO 10 I=1,M
      IF(X(I,J).LT.0.000000001)GO TO 10
      ROW(J)=ROW(J)+COLA(I)*X(I,J)
      RN=RN+X(I,J)
   10 CONTINUE
   11 ROW(J)=ROW(J)/RN
      DO 13 I=1,M
      COLA(I)=0.
      RN=0.
      DO 12 J=1,N
      IF(X(I,J).LT.0.000000001)GO TO 12
      COLA(I)=COLA(I)+ROW(J)*X(I,J)
      RN=RN+X(I,J)
   12 CONTINUE
   13 COLA(I)=COLA(I)/RN
   32 COLMAX=-1.E200
      COLMIN=1.E200
      DO 15 I=1,M
      IF(COLA(I).LT.COLMIN)COLMIN=COLA(I)
   15 IF(COLA(I).GT.COLMAX)COLMAX=COLA(I)
      DO 16 I=1,M
   16 COLA(I)=100.*(COLA(I)-COLMIN)/(COLMAX-COLMIN)
      IF(LOOP.EQ.1.OR.IRED.EQ.1)GO TO 37
      GO TO 21
   41 IRED=0
C CALCULATE REDUCTION FACTOR (F) TO ALLOW FOR FIRST AXIS
      SXY(1)=0.
      SXY(2)=0.
      DO 34 I=1,M
   34 SXY(1)=SXY(1)+XX(I,1)*COLA(I)
```

```
      F(1)=SXY(1)/SXZ(1)
      IF(LOOP.EQ.3)GOTO72
      DO35I=1,M
   35 COLA(I)=COLA(I)-F(1)*Z(I,1)
      GOTO32
   72 DO81I=1,M
   81 SXY(2)=SXY(2)+XX(I,2)*COLA(I)
      F(2)=SXY(2)/SXZ(2)
      DO74I=1,M
   74 COLA(I)=COLA(I)-F(1)*Z(I,1)-F(2)*Z(I,2)
      GOTO32
   37 DO 17 I=1,M
      DIFF=ABS(COLA(I)-COLB(I))
      IF(DIFF.GT.0.01)GOTO18
   17 CONTINUE
      GO TO 20
   18 DO 19 I=1,M
   19 COLB(I)=COLA(I)
      IF(IRED.EQ.1.AND.LOOP.GT.1)GOTO41
      GO TO 21
   20 WRITE(6,22)IT
   22 FORMAT(/* NUMBER OF ITERATIONS =*,I4)
      EIG=(COLMAX-COLMIN)/100.
      WRITE(6,23)EIG
   23 FORMAT(/* ESTIMATE OF EIGEN VALUE =*,F10.5)
      ROWMAX=0.
      ROWMIN=1.E200
      DO 24 J=1,N
      IF(ROW(J).LT.ROWMIN)ROWMIN=ROW(J)
   24 IF(ROW(J).GT.ROWMAX)ROWMAX=ROW(J)
      DO 25 J=1,N
   25 ROW(J)=100.*(ROW(J)-ROWMIN)/(ROWMAX-ROWMIN)
      WRITE(6,26)
   26 FORMAT(/* STAND COORDINATES -*)
      K=LOOP
      DO66J=1,N
   66 IROW(J,K)=IFIX(ROW(J)+0.5)
      WRITE(6,27)(IROW(J,K),J=1,N)
   27 FORMAT(10I12)
      WRITE(6,33)
   33 FORMAT(/* ATTRIBUTE COORDINATES*)
      DO67I=1,M
   67 ICOLA(I,K)=IFIX(COLA(I)+0.5)
      WRITE(6,27)(ICOLA(I,K),I=1,M)
      IF(LOOP.EQ.3)GOTO51
      IF(LOOP.EQ.2)GOTO101
      WRITE(6,39)
   39 FORMAT(//* S E C O N D  A X I S*)
      GOTO102
  101 WRITE(6,103)
  103 FORMAT(//1X,*T H I R D  A X I S*)
  102 LP=LOOP
      LOOP=LOOP+1
C BEGIN CALCULATION OF REDUCTION FACTOR TO ALLOW FOR FIRST AXIS
      SRZ(LP)=0.
      DO 28 I=1,M
      Z(I,LP)=COLA(I)
      RZ(I,LP)=R(I)*Z(I,LP)
   28 SRZ(LP)=SRZ(LP)+RZ(I,LP)
      DO 29 I=1,M
   29 XX(I,LP)=RZ(I,LP)-R(I)*SRZ(LP)/SR
      SXZ(LP)=0.
      DO 30 I=1,M
   30 SXZ(LP)=SXZ(LP)+XX(I,LP)*Z(I,LP)
      DO 40 I=1,M
      COLA(I)=COLB(I)
   40 COLB(I)=0.
      GO TO 31
   51 CALL PHOMB
      STOP
      END
```

```
      SUBROUTINE RHOMB
      COMMON/A/IROW(100,3),ICOLA(100,3),M,N
      COMMON/C/XA(100),Y(100),IZ(100),IALPHA(26)
      DIMENSION IXPLOT(100,2)
      DATA IEX,(IALPHA(I),I=1,26)/1H=,1H*,1HB,1HC,1HD,1HE,1HF,1HG,1HH,1HI
     1,1HJ,1HK,1HL,1HM,1HN,1HO,1HP,1HQ,1HR,1HS,1HT,1HU,1HV,1HW,1HX,1HY,1
     1HZ/
      DO43NK=1,2
      DO22I=1,3
      GOTO(23,24,25)I
   23 NI=1
      NO=2
      GOTO26
   24 NI=3
      NO=1
      GOTO26
   25 NI=3
      NO=2
   26 IF(NK.EQ.2)GOTO34
      JM=N
      DO57J=1,N
      IXPLOT(J,1)=IROW(J,NI)
   57 IXPLOT(J,2)=IROW(J,NO)
      GOTO32
   34 JM=M
      DO31J=1,M
      IXPLOT(J,1)=ICOLA(J,NI)
   31 IXPLOT(J,2)=ICOLA(J,NO)
C     OVERLAYS.................
   32 DO1K=1,JM
      IZ(K)=1
      IK=K+1
      DO1J=IK,JM
      IF(IXPLOT(K,1).EQ.101)GOTO4
      IF(IXPLOT(K,1).EQ.IXPLOT(J,1).AND.IXPLOT(K,2).EQ.IXPLOT(J,2))GOTO2
      GOTO1
    2 IXPLOT(J,1)=101
      IXPLOT(J,2)=101
      IZ(K)=IZ(K)+1
      GOTO1
    4 IZ(K)=0
    1 CONTINUE
      DO5J=1,JM
      XA(J)=FLOAT(IXPLOT(J,1))/10.0
      Y(J)=FLOAT(IXPLOT(J,2))/10.0
      IF(IZ(J).EQ.0)GOTO5
      IF(IZ(J).GT.26)GOTO6
      ID=IZ(J)
      IZ(J)=IALPHA(ID)
      GOTO5
    6 IZ(J)=IEX
    5 CONTINUE
      DO21J=1,JM
C     TRANSFORM TO RHOMB 1
      Y(J)=Y(J)-XA(J)*0.5
      XA(J)=XA(J)*0.866
C     DETERMINE FURTHER PROCESSING
      GOTO(21,33,41)I
C     TRANSFORM TO RHOMB 2
   33 IF(XA(J).EQ.0.0)XA(J)=0.00001
      IF(Y(J).EQ.0.0)Y(J)=0.00001
      RAD=240.0*0.01745329
      XNEW=XA(J)*COS(RAD)-Y(J)*SIN(RAD)
      YNEW=XA(J)*SIN(RAD)+Y(J)*COS(RAD)
      XA(J)=XNEW
      Y(J)=YNEW
      GOTO21
C     TRANSFORM TO RHOMB 3
   41 XA(J)=-XA(J)
   21 CONTINUE
   22 CALL RPLOT(I,NK,IEX,JM)
   43 CONTINUE
      RETURN
      END
```

```
      SUBROUTINE RPLOT(I,NK,IEX,JM)
      COMMON/B/ITITLE(8)
      COMMON/C/XA(100),Y(100),IZ(100),IALPHA(26)
      IF(I.GT.1)GOTO7
      IF(NK.GT.1)GOTO2
      CALL START(1)
      CALL BORDOFF
      CALL NEWPAGE
    2 CALL SYMBOL(5.64,0.0,0.42,ITITLE,0.0,80)
      IF(NK.EQ.2)GOTO4
      CALL SYMBOL(5.64,20.72,0.42,'STAND PLOT',0.0,10)
      GOTO5
    4 CALL SYMBOL(5.64,20.72,0.42,'ATTRIBUTE PLOT',0.0,14)
    5 CALL PLOT(14.3,10.72,-3)
      CALL PLOT(0.0,10.0,2)
      CALL PLOT(8.66,5.0,2)
      CALL PLOT(8.66,-5.0,2)
      CALL PLOT(0.0,-10.0,2)
      CALL PLOT(-8.66,-5.0,2)
      CALL PLOT(-8.66,5.0,2)
      CALL PLOT(0.0,10.0,2)
      CALL PLOT(0.0,0.0,-2)
      CALL PLOT(-8.66,-5.0,2)
      CALL PLOT(0.0,0.0,-2)
      CALL PLOT(8.66,-5.0,2)
      CALL SYMBOL(-0.125,10.2,0.42,56,0.0,-1)
      CALL SYMBOL(8.5,-5.36,0.42,55,0.0,-1)
      CALL SYMBOL(-9.05,-5.36,0.42,57,0.0,-1)
      CALL PLOT(-0.025,-0.05,-3)
    7 DO6J=1,JM
      IF(IZ(J).EQ.0)GOTO6
      CALL SYMBOL(XA(J),Y(J),0.1,IZ(J),0.0,1)
    6 CONTINUE
      IF(I.EQ.3.AND.NK.EQ.2)GOTO8
      IF(NK.EQ.2)GOTO1
      IF(I.EQ.3)CALL NEWPAGE
      CALL BORDOFF
      GOTO1
    8 CALL ENPLOT
    1 CONTINUE
      RETURN
      END
```

Fig. 104. Histogram presentation of the abundance of plant remains recovered from section 1, Hasty Bank. This figure, and Figs. 105 and 106, are based on the log dominance/density scale as used by C.R. Hill and is shown in table 5. All quadrat counts have been referred to a sample volume of 50 x 50 x 20 cm^3. (After C.R. Hill, 1974)

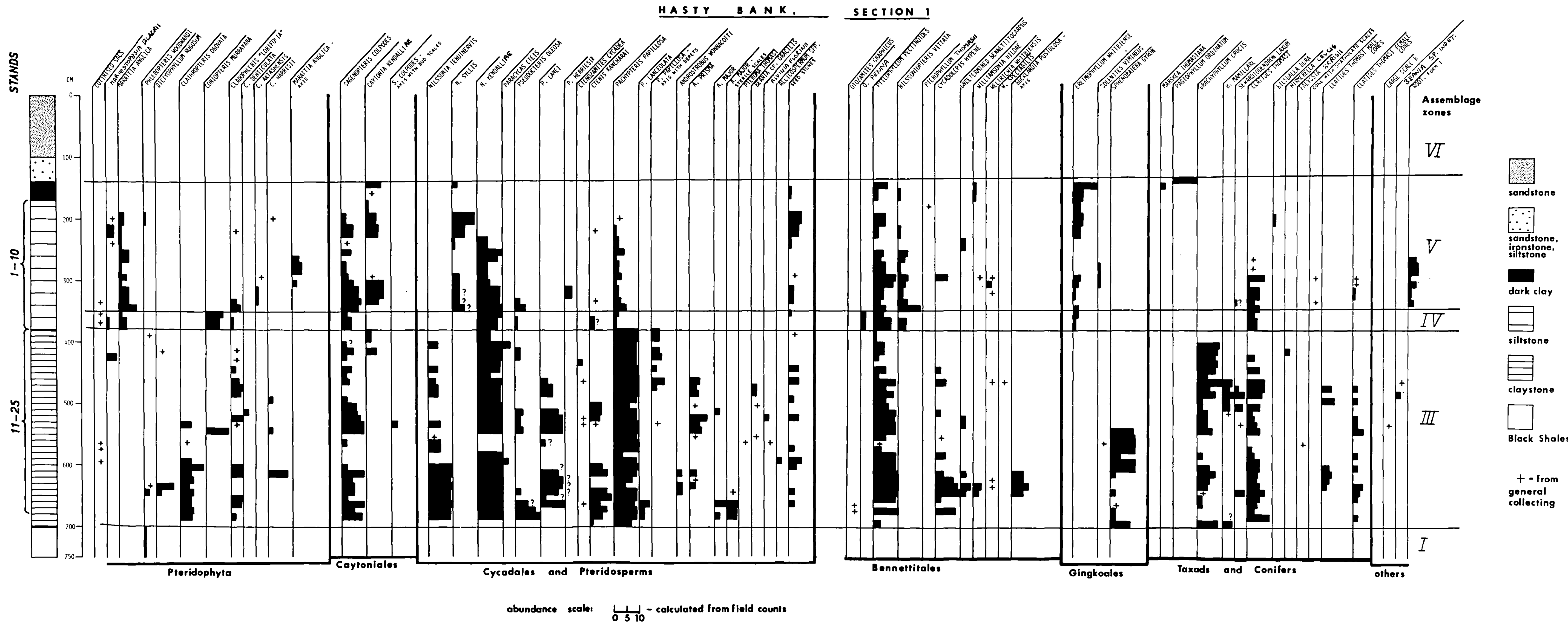
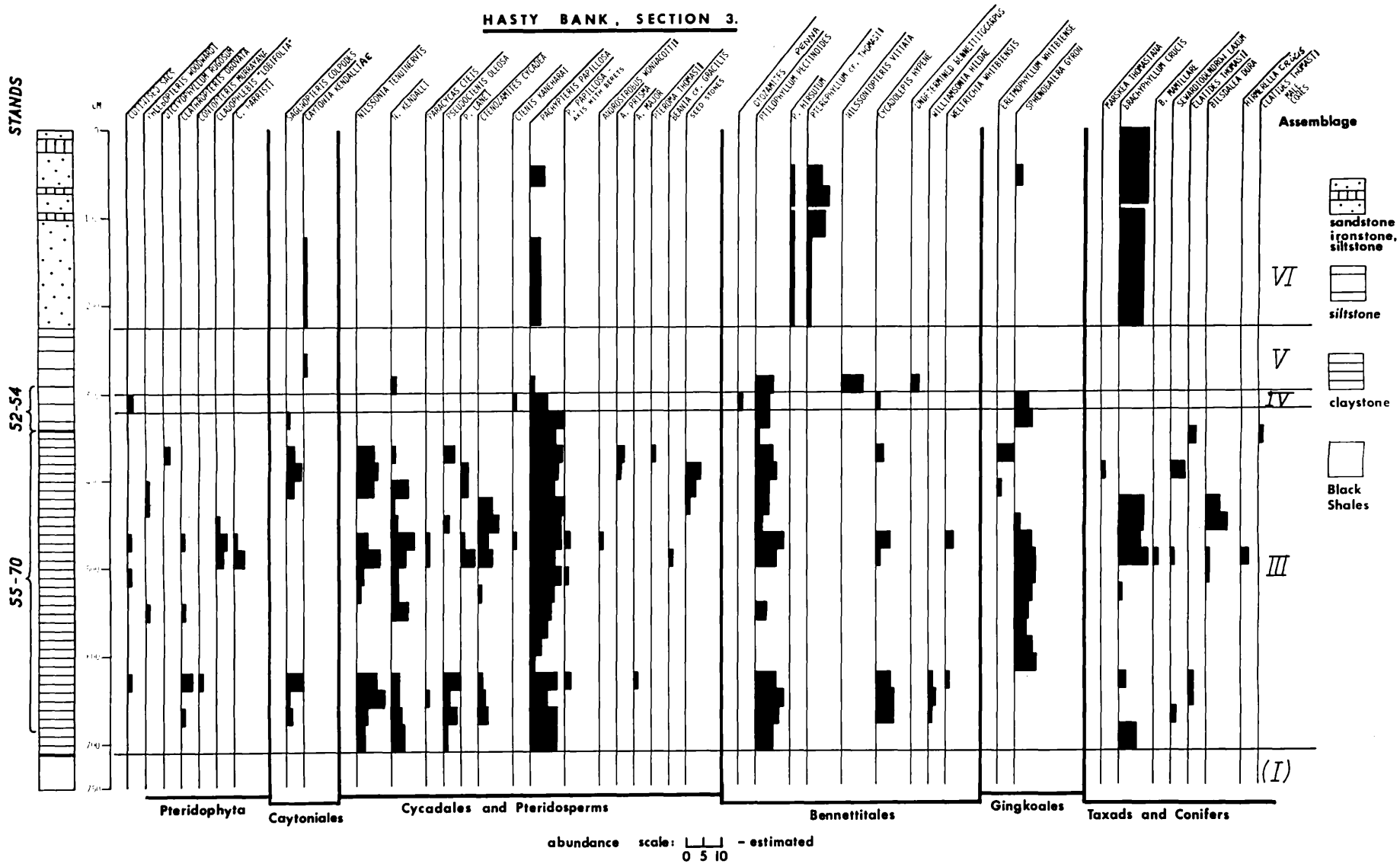

HASTY BANK. SECTION 1
STANDS
1–10
11–25
CM
0
100
200
300
400
500
600
700
750
Assemblage zones
VI
V
IV
III
I
sandstone
sandstone, ironstone, siltstone
dark clay
siltstone
claystone
Black Shales
+ = from general collecting
Pteridophyta
Caytoniales
Cycadales and Pteridosperms
Bennettitales
Gingkoales
Taxads and Conifers
others
abundance scale: 0 5 10 – calculated from field counts

Fig. 105. Histogram presentation of the abundances of plant remains from Hasty Bank section 2. (After C.R. Hill, 1974)


HASTY BANK. SECTION 2.
STANDS
26-46
47-51
CM
0
100
200
300
400
500
600
700
750
CUTINIZED SACS
MARESNOPTERIS GLACILIS
MARATTIA ANGUSTA
PHLEBOPTERIS WOODWARDII
DICTYOPHYLLUM RUGOSUM
CLATHROPTERIS MENISCOIDES
STANGERIOPTERIS GRANATA
DICKSONIA KENDALLIAE
COMPTOPTERIS SITTONS
CLADOPHLEBIS NORMANNI
C. NARMSTII
MARATTIA ANGUSTA AXIS
SAGENOPTERIS COLPHENSIS
CAYTONIA KENDALLIAE
NILSSONIA TENUINERVIS
N. STILUS
N. KENDALLIAE
PARACYCAS CUTTS
PSEUDOCTENIS CUTTSA
P. TENUIS
CTENOZAMITES CYCADEA
CTENIS KANSANAENSIS
PACHYPTERIS PAPILLOSA
P. PAPILLOSA AXIS WITH REPLETS
ANOMOZAMITES NORMANDITI
A. ANOMALUS
PTERONIA THOMASII
BENNIA cf. GRACILIS
ALLOSPERMOPHYTON SPP.
SEED STROBES
OTOZAMITES REVOLUTA
TYRIDOPHYLLUM cf. THOMASII
PTILOPHYLLUM PECTINOIDES
P. INTERMEDIUM
CYCADOPTERIS VITTATA
C. SPINIFOLIUS
WILLIAMSONIA FULGENS
WILLIAMSONIA SPECTABILIS
CARLOPHYLLUM WHITEHOUSE
SPHENOBAIERA GYROPHYLLOIDES
BRACHYPHYLLUM CRUCIS
B. MAMILLARE
CLATHRUS THOMASII
SILSSALIA DUNI
ARAUCARITES PHILLIPSII
BRACHYPHYLLUM MAMILLARE WELL COPY
CLATHRUS THOMASII WELL COPY
LARGE SCALE L
ROOT, max 2
Assemblage
V
IV
III
II
dark clay
sandstone
siltstone
claystone
Black Shales
+ from general collecting
Pteridophyta
Caytoniales
Cycadales and Pteridosperms
Bennettitales
Gingkoales
Conifers
other
abundance scale: -estimated
0 5 10

106. Hasty Bank, section 3, histograms (After C.R. Hill, 1974)


HASTY BANK, SECTION 3.
STANDS
52-54
55-70
Assemblage
VI
V
IV
III
(I)
sandstone ironstone, siltstone
siltstone
claystone
Black Shales
Pteridophyta
Caytoniales
Cycadales and Pteridosperms
Bennettitales
Gingkoales
Taxads and Conifers
abundance scale: 0 5 10 - estimated

REFERENCES

ANDERSEN, S.TH. (1970) The relative pollen productivity of north European trees, and correction factors for tree pollen spectra. Daum. geol. Unders. Ser. II 96, 99pp.

ANDERSEN, S.TH. (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 Ed. H.J.B. BIRKS and R.G. WEST 14th Symposium of the British Ecological Society. Blackwell Scientific Publications.

AUTEN, J.T. (1941) Black locust, pines and sassafras as builders of forest soil. Tech. notes cent St. For. Exp. Sta. 32, 9pp.

BATCHELOR, G.K. (1970) An Introduction to Fluid Dynamics, Cambridge University Press. 615pp.

BEAMAN, D.R. and ISASI, J.A. (1972) Electron Beam Microanalysis American Society for Testing and Materials Special technical publication, 506, 80pp.

BENOIT, R.E., STARKEY, R.L. and BASARABA, J. (1968) Effect of purified plant tannin on the decomposition of some organic compounds and plant materials. Soil Sci. 105 (3), 153-158.

BERRY, E.W. (1906) Leaf Rafts and Fossil Leaves. Torreya, New York, 6, 246-249.

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. 14th Symposium of the British Ecological Society. Blackwell Scientific Publications.

BIRKS, H.J.B. (1973) Modern pollen rain studies in some arctic and alpine environments. In Quaternary Plant Ecology, Ed. H.J.B.BIRKS and R.G. WEST. 14th Symposium of the British Ecological Society. Blackwell Scientific Publications.

BLACKITH, R.E. and REYMENT, R.A. (1971) Multivariate Morphometrics. Academic Press. London and New York. 411pp.

BONNEVIE-SVENDSEN, C. and GJEMS, O. (1957) Amount and chemical composition of the litter from Larch, beech, Norway spruce and Scots pine stands and its effect on the soil. Meddr. norske. Skogsfors Ves. 48, 111-174.

BRAY, J.R. and GORHAM, E. (1964) Litter production in forests of the World. Adv. Ecol. Res. 2, 101-158.

BROWN, S.R. (1956) A piston sampler for surface sediments of lake deposits. Ecology. 37, 611-613.

CAMPBELL, R.C. (1967) Statistics for Biologists. Cambridge University Press. 242pp.

CHANDLER, M.E.J. (1964) The Lower Tertiary Floras of Southern England IV. A summary and survey of findings in the light of recent botanical observations. British Museum (Natural History) London.

CHANEY, R.W. (1924) Quantitative Studies of the Bridge Creek Flora. Am. Jour. Sci. 8, 127-144.

CHANEY, R.W. and SANBORN, E. (1933) The Goschen Flora of West Central Oregon. Carnegie Inst. Wash. Publ. 439, 1-103.

COEY, J.M.D. and READMAN, P.W. (1973) Characterization and magnetic properties of natural ferric gel. Earth and Planetary Science Letters, 21, 45-51.

COMANOR, P.L. (1968) Forest Vegetation and the Pollen spectrum: an examination of the usefulness of the R value. Bull. New. Jers. Acad. Sci. 13, 7-19.

CUMMINS, K.W., PETERSEN, R.C., HOWARD, F.O., WUYCHECK, J.C. and HOLT, V.I. (1973) The utilization of leaf litter by stream detritivores. Ecology, 54, 336-345.

CUMMINS, K.W., KLUG, M.J., WETZEL, R.G., PETERSEN, R.C., SUBERKROPP, K.F., MANNY, B.A., WUYCHECK, J.C. and HOWARD, F.O. (1972) Organic enrichment with leaf leachate in experimental lotic ecosystems. Bioscience, 22, 719-722.

CUSHING, E.J. and WRIGHT, H.E. Jr. (1965) Hand operated piston corers for lake sediments. Ecology, 46, 380-384.

DALE, M.B. and WALKER, D. (1970) Information analysis of pollen diagrams. Pollen et. Spores, 12 (1), 22-37.

DAVIS, J.C. (1973) Statistics and Data Analysis in Geology, John Wiley and Sons Inc. 550pp.

DAVIS, M.B. (1963) On the theory of pollen analysis. Am. J. Sci. 261, 897-912.

DAVIS, M.B. (1969) Palynology and Environmental History during the Quaternary period. Am. Sci. 57, 317-32.

De VRIES, H., BREDEMEIJER, G. and HEINEN, W. (1967) Decay of cutin and cuticular compounds by soil microorganisms in their natural environment. Acta. Botn. Neerl. 16 (3), 102-110.

DILCHER, D.L. (1971) A revision of the Eocene Flora of Southeastern North America. The Palaeobotanist, 20, 7-18.

DILCHER, D.L. (1973) A palaeoclimatic Interpretation of the Eocene Floras of Southeastern North America. In Vegetation and Vegetational History of Northern Latin America. Ed. A. GRAHAM. Elsevier Scientific Publishing Company, Amsterdam, London, New York. pp.39-59.

ECHLIN, P. and MORETON, R.B. (1973) The preparation, coating and examination of frozen biological materials in the scanning electron microscope. Proc. 6th Annual S.E.M. Symposium II Reseach Institute, Ed. O. JOHARI. pp.325-332.

ECHLIN, P. and MORETON, R.B. (1974) The preparation of biological materials for X-ray microanalysis. In Microprobe Analysis as Applied to Cells and Tissues, Ed. T.A. HALL, P. ECHLIN and R. KAUFMANN, Academic Press. 435pp.

EGGLISHAW, H.J. (1964) The distributional relationships between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33, 463-476.

FAEGRI, K. (1966) Some problems of representativity in Pollen analysis. Palaeobot. 15, 135-140.

FERGUSON, D.K. (1971) The miocene flora of Kreuzau Western Germany. 1: The Leaf Remains. North Holland Publishing Company Amsterdam and London, 297pp.

FINNEY, D.J. (1971) Probit Analysis. Cambridge University Press, 333pp.

FISHER, Sir RONALD A. and YATES, F. (1963) Statistical tables for Biological, Agricultural and Medical Research. 6th Edition. Oliver and Boyd. Edinburgh and London.

GOODALL, D.W. (1952) Some considerations in the use of point quadrats for the analysis of vegetation. Aust. J. Sci. Res. Ser. B 5, 1-41.

GOWER, J.C. (1966) Some distance properties of latent root vector methods used in Multivariate analysis. Biometrika, 53, 325-338.

GREIG-SMITH, P. (1964) Quantitative Plant Ecology. 2nd Edition. Butterworths, London. 256pp.

HALL, T.A. (1968) The Quantitative Electron Probe Microanalysis. Ed. K.F.J. HEINRICH. N.B.S. Special Publ. 298, 269-299.

HALL, T.A. (1971) The microprobe assay of chemical elements. In Physical Techniques in Biological Research. Ed. G. OSLER. Academic Press, 157-275.

HALL, T.A. and GUPTA, B.L. (1974) Measurement of mass loss in biological specimens under an electron microbeam. In Microprobe Analysis as Applied to Cells and Tissues. Ed. T.A. HALL, P. ECHLIN and R. KAUFMANN, Academic Press. 435pp.

HARRIS, T.M. (1969) The Yorkshire Jurassic Flora III Bennettitales British Museum (Natural History) London.

HARRIS, T.M., MILLINGTON, W., MILLER, J. (1974) The Yorkshire Jurassic

Flora, IV Ginkgoales and Czekanowskiales Part 1 Ginkgoales. British Museum (Natural History) London.

HILL, C.R. (1974) Palaeobotanical and Sedimentological Studies on the Lower Bajocian (Middle Jurassic) Flora of Yorkshire. PhD thesis. Leeds University.

HILL, M.O. (1973) Reciprocal Averaging: An Eigenvector Method of Ordination. J. Ecol. 61, 237-249.

HILL, M.O. (1974) Correspondence Analysis: A neglected Multivariate Method. Appl. Statistics, 23 (3), 340-354.

HUGHES, M.K. (1971) Tree biocontent, net production and litter fall in deciduous woodland. Oikos, 22 (1), 62-73.

HUTCHINSON, D.E. (1957) A treatise on limnology Vol. I, Geography, Physics and Chemistry. John Wiley and Sons Inc, New York, 1015pp.

HUTCHINSON, T.E., BACANER, M., BROADHURST, J. and LILLEY, J. (1974) Elemental Microanalysis of Frozen Biological Thin Sections by Scanning Electron Microscopy and Energy Selective X-ray Analysis. In Microprobe Analysis as Applied to Cells and Tissues. Ed. T.A. HALL, P. ECHLIN and R. KAUFMANN. Academic Press. 435pp.

HYNES, H.B.N. (1961) The Invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol., 57, 344-388.

JANSSEN, C.R. (1967) A comparison between regional pollen rain and the sub-recent vegetation in four major vegetation types in Minnesota (U.S.A.). Rev. Palaeobotan. Palynol., 2, 331-342.

KERRICK, D.M., EMINHIZER, L.B. and VILLAUME, J.F. (1973) The Role of Carbon Film Thickness in Electron Microprobe Analysis. American Mineralogist, 58, 920-925.

KRASILOV, V.A. (1969) Types of palaeofloristic successions and their causes. Paleont. Jour., 3, 296-308.

LAMBERT, J.M. and DALE, M.B. (1964) The use of Statistics in Phytosociology. Adv. Ecol. Res., 2, 59-99.

LAWLEY, D.N. and MAXWELL, A.E. (1963) Factor Analysis as a Statistical Method. Butterworths, London, 117pp.

LIVINGSTONE, D.A. (1955) A lightweight piston sampler for lake deposits. Ecology, 36, 137-139.

MacGINITIE, M.D. (1953) Fossil plants of the Florissant beds, Colorado. Carnegie Inst. Wash. Publ. 599, 1-198.

McQUEEN, D.R. (1969) Macroscopic plant remains in Recent lake sediments. Tuatara, 17, 13-19.

MANTZ, P.A. (1973) Cohesionless, Fine Graded Flaked Sediment Transport by Water. Nature Physical Science, 246, 14-16.

MATHEWS, C.P. and KAWALCZESKI, A. (1969) Disappearance of leaf litter and its contribution to production in the River Thames. J. Ecol. 57, 543-552.

MELIN, E. (1930) Biological decomposition of some types of litter from North American Forests. Ecology, 11, 72-101.

MOSELEY, H.N. (1892) Notes by a Naturalist on the 'Challenger' 2nd Edition. XXIV + 540pp. London.

MUIR, M.D. (1974) Fundamentals of the S.E.M. for biologists. Proc. 7th I.I.T. Research Institute Scanning Electron Microscope Symposium Chicago, 1011-1018.

MUIR, M.D., HAMILTON, L.H., GRANT, P.R. and SPICER, R.A. (1974) A comparative study of modern and fossil microbes using X-ray micro-analysis and Cathodoluminescence. In Microprobe Analysis as Applied to Cells and Tissues. Ed. T.A. HALL, P. ECHLIN and R. KAUFMANN, Academic Press, 435pp.

MUIR, M.D., SPICER, R.A., GRANT, P.R. and GIDDENS, R. (1974) X-ray microanalysis in the S.E.M. for the determination of elements in Modern and Fossil Microorganisms. In Eighth International Congress on Electron Microscopy, Canberra, Vol. II, 104-105.

MULLER, J. (1959) Palynology of Recent Orinocco Delta and Shelf Sediments. Micropalaeontology, 5 , 1-32.

NEWBOULD, P.J. (1967) Methods for estimating the Primary Production of Forests, I.B.P. Handbook No. 2. 62pp. Blackwell, Oxford.

NYKVIST, N. (1962) Leaching and Decomposition of litter V. Experiments on leaf litter of Alnus glutinosa, Fagus sylvatica, Quercus robur. Oikos, 13, 232-248.

OLDFIELD, F. (1970) Some aspects of scale and complexity in pollen analytically based Palaeoecology. Pollen et Spores, 12 (2), 163-171.

ORLOCI, L. (1966) Geometric models in Ecology I. The theory and application of some ordination methods. J. Ecol., 54, 193-215.

ORLOCI, L. (1968) Information analysis in Phytosociology. J. Theoret. Biol., 20, 271-284.

ORLOCI, L. (1975) Multivariate Analysis in Vegetation Research, Junk, Amsterdam, 276pp.

O'SULLIVAN, P.E. and RILEY, D.H. (1974) Multivariate numerical analysis of surface pollen spectra from a native Scots pine forest. Pollen et Spores, 16 (2), 239-264.

OTTO, G.H. (1938) The sedimentation unit and its use in field sampling. The Journal of Geology, 46, 569-582.

PANG, Y.H. (1939) Mitteilungen der Preussischen Versuchsanstalt fur

Wasser-erd-und Schiffbau, Berlin, No. 37.

PECK, R.M. (1973) Pollen budget studies in a small Yorkshire Catchment. In Quaternary Plant Ecology. Ed. H.J.B. BIRKS and R.G. WEST. 14th Symposium of the British Ecological Society. Blackwell Scientific Publication.

PETERSEN, R.C. and CUMMINS, K.W. (1974) Leaf processing in a Woodland Stream. Freshwater Biology, 4 (4), 343-368.

REID, E.M. and CHANDLER, M.E.J. (1933) The flora of the London Clay. British Museum (Natural History) London. 561pp

REYMENT, R.A. (1969) Interstitial ecology of the Niger Delta: an Actuopalaeoecological study. Bull. Geol. Instn. Univ. Uppsala, 1, 121-159.

REYMENT, R.A. (1971) An introduction to Quantitative Palaeoecology, Elsevier, Amsterdam, 226pp.

RICHARDS, P.W. (1952) The tropical rain forest. Univ. Cambridge Press, Cambridge, Mass., 450pp.

RIDLEY, H.N. (1930) The dispersal of Plants throughout the World. L. Reave & Co. Ltd., Ashford, Kent.

ROSENTIEL, A.V.P., HOHLING, M.J., SCHNERMANN, J. and KRIZ, W. (1970) Proc. 5th Natl. Conf. Electron Probe Analysis, Electron Probe Analysis Society of America, New York City, 33A-33B.

ROWLEY, J.R. and DAHL, A.O. (1956) Modifications in design and use of the Livingstone piston sampler. Ecology, 37, 849-851.

SCHOKLITSH, A. (1914) Uber Schleppkraft und Geschiebebewegung, Engelman, Leipzig.

SELLEY, R.C. (1971) Ancient Sedimentary Environments, Ithaca N.Y. Cornell Univ. Press, 240pp.

SHIELDS, A. (1936) Mitteilungen der Preuss. Versuchsaust fur Wasserbau und Schiffbau, Berlin, No. 26.

SMITH, I.R. (1975) Turbulence in lakes and rivers. Freshwater Biological Association Scientific Publication Mo. 29.

SPICER, R.A. GRANT, P.R. and MUIR, M.D. (1974) An Inexpensive portable freeze-drying unit for S.E.M. specimen preparation. Proc. 7th I.I.T. Research Institute Scanning Electron Microscope Symposium Chicago, 299-304.

SPURR, A.R. (1974) Macrocyclic Polyether Complexes with Alkali Elements in epoxy resin as standards for X-ray analysis of Biological Tissues. In Microprobe Analysis as Applied to Cells and Tissues. Ed. T.A. HALL, P. ECHLIN and R. KAUFMANN, Academic Press. 435pp.

Wasser-erd-und Schiffbau, Berlin, No. 37.

PECK, R.M. (1973) Pollen budget studies in a small Yorkshire Catchment. In Quaternary Plant Ecology. Ed. H.J.B. BIRKS and R.G. WEST. 14th Symposium of the British Ecological Society. Blackwell Scientific Publication.

PETERSEN, R.C. and CUMMINS, K.W. (1974) Leaf processing in a Woodland Stream. Freshwater Biology, 4 (4), 343-368.

REID, E.M. and CHANDLER, M.E.J. (1933) The flora of the London Clay. British Museum (Natural History) London. 561pp

REYMENT, R.A. (1969) Interstitial ecology of the Niger Delta: an Actuopalaeoecological study. Bull. Geol. Instn. Univ. Uppsala, 1, 121-159.

REYMENT, R.A. (1971) An introduction to Quantitative Palaeoecology, Elsevier, Amsterdam, 226pp.

RICHARDS, P.W. (1952) The tropical rain forest. Univ. Cambridge Press, Cambridge, Mass., 450pp.

RIDLEY, H.N. (1930) The dispersal of Plants throughout the World. L. Reave & Co. Ltd., Ashford, Kent.

ROSENTIEL, A.V.P., HOHLING, M.J., SCHNERMANN, J. and KRIZ, W. (1970) Proc. 5th Natl. Conf. Electron Probe Analysis, Electron Probe Analysis Society of America, New York City, 33A-33B.

RUSS, J. C. (1974) The direct element ratio model for quantitative analysis of thin sections, In Microprobe Analysis as Applied to Cells and Tissues, Ed. T. A. HALL, P. ECHLIN and R. KAUFMANN. Academic Press. 435pp.

Cornell Univ. Press, 240pp.

SHIELDS, A. (1936) Mitteilungen der Preuss. Versuchsaust fur Wasserbau und Schiffbau, Berlin, No. 26.

SMITH, I.R. (1975) Turbulence in lakes and rivers. Freshwater Biological Association Scientific Publication Mo. 29.

SPICER, R.A. GRANT, P.R. and MUIR, M.D. (1974) An Inexpensive portable freeze-drying unit for S.E.M. specimen preparation. Proc. 7th I.I.T. Research Institute Scanning Electron Microscope Symposium Chicago, 299-304.

SPURR, A.R. (1974) Macrocyclic Polyether Complexes with Alkali Elements in epoxy resin as standards for X-ray analysis of Biological Tissues. In Microprobe Analysis as Applied to Cells and Tissues. Ed. T.A. HALL, P. ECHLIN and R. KAUFMANN, Academic Press. 435pp.

TAUBER, M. (1965) Differential pollen dispersal and the Interpretation of pollen diagrams. Danm. geol. Unders. Ser. II, 89, 69pp.

TAUBER, M. (1967) Investigations of the mode of pollen transfer in forested areas. Rev. Palaeobotan. Palynol. 3, 277-286.

TRAVERSE, A. and GINSBURG, R.N. (1966) Palynology of the surface sediments of the Great Bahama Bank as related to water movements and sedimentation. Marine Geol., 4, 417-459.

VALLENTYNE, J.R. (1955) A modification of the Livingstone piston sampler for lake deposits. Ecology, 36, 139-141.

WAKSMAN, S.A. and TENNY, F.G. (1927) The composition of natural organic materials and their decomposition in the soil. I. Methods of Quantitative analysis of plant material. Soil Sci., 24, 275-283.

WAKSMAN, S.A., TENNY, F.G. and STEVENS, K.R. (1928) The role of microorganisms in the transformation of organic matter in forest soils. Ecology, 9, 126-144.

WARNER, R.R. and COLEMAN, J.R. (1974) Quantitative Analysis of Biological Materials using Computer Correction of X-ray intensities. In Microprobe Analysis as Applied to Cells and Tissues. Ed. T.A. HALL, P. ECHLIN and R. KAUFMANN, Academic Press, 435pp.

WATTS, W.A. and WINTER, T.C. (1966) Plant macrofossils from Kirchner Marsh, Minnesota - a palaeoecological study. Bull. Geol. Soc. Am. 77, 1339-1360.

WHITE, D. (1933) Role of water conditions in the Formation and Differentiation of Common (Banded) Coals. Economic Geology, 28, 556-570.

WILLIAMS, A.M. (1963) The Enzyme Chemistry of Phenolic Compounds. Ed. J.B. PRIDHAM. pp.87-95. Pergamon, Oxford and MacMillan, New York.

WOLFE, J.A. (1969) Neogene floristic and vegetational history of the Pacific Northwest. Madroño, 20, 83-110.

WOLFE, J.A. (1971) Tertiary Climatic fluctuations and methods of analysis of Tertiary floras. Palaeogeogr. Palaeoclimatol. Palaeoecol., 9, 27-57.