

The Sorting and Deposition of
Allochthonous Plant Material in a
Modern Environment at Silwood Lake,
Silwood Park, Berkshire, England

GEOLOGICAL SURVEY PROFESSIONAL PAPER 1143



The Sorting and Deposition of Allochthonous Plant Material in a Modern Environment at Silwood Lake, Silwood Park, Berkshire, England

By ROBERT A. SPICER

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*A study of how a potential plant-fossil deposit
was formed in a fluviolacustrine environment*



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THE SORTING AND DEPOSITION OF ALLOCHTHONOUS PLANT MATERIAL IN A MODERN ENVIRONMENT AT SILWOOD LAKE, SILWOOD PARK, BERKSHIRE, ENGLAND

By ROBERT A. SPICER

ABSTRACT

Quantitative statistical sampling of plant debris entombed within deltaic sediments of a Holocene fluviolacustrine environment at Silwood Lake, Berkshire, demonstrates that patterns of deposition exist that can be used to reconstruct the relative spatial distributions of species within the source vegetation.

Samples of unconsolidated sediment, each $0.5 \times 0.5 \times 0.02$ m in volume, were collected from subaerial deltaic deposits, using a regular sampling matrix, and examined for their content of plant material. Density and cover measurements were made of both whole and fragmented recovered leaves and the data subsequently analyzed using principal components analysis and correspondence analysis ordination methods. Both theoretically and practically, correspondence analysis proved the more useful technique and revealed that the pattern of fragment deposition, unlike that of whole leaves, is associated with stream distributaries. The various species compositions of the whole-leaf and fragmented-leaf distribution over a single bedding surface can be used to reconstruct the relative positions of the source species within the vegetation.

Sorting by long-distance wind transport favors small sun leaves; in open-lake environments the deposited leaf size population can depart significantly from that exhibited by the growing source vegetation.

The vertical pattern of plant-debris deposition was revealed by coring. A lower leaf bed represents lake-bottom deposition, an upper leaf bed was formed by direct aerial transport of leaves, fruits, seeds, and other material to the subaerial deltaic sediments as well as by collective settling at the top of the foreset slope of stream-transported material. Theoretically, these two distinct leaf beds differ in species composition such that the lower leaf bed reflects the vegetation immediately surrounding the basin of deposition, and the upper a deposit enriched by plant material derived from more distantly growing upstream vegetation. Preferential feeding by invertebrate organisms and differential microbiological breakdown may seriously distort this pattern, but the effect may be compensated for by examining leaves preserved in relation to rapidly deposited sediments. Rapid deposition limits the biological degradation that can take place and that may totally destroy susceptible species under more normal conditions.

Most information of paleoecological value is in the fragmented material rather than the more complete "museum specimens." Vertical differences in the species composition of plant-fossil beds may reflect special species distributions in the source vegetation rather than floristic changes with time.

INTRODUCTION

The development of any science follows a process of gradual change from a qualitative to a quantitative approach, and in this respect paleobotany is no excep-

tion. 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, leading to the development of techniques that enable us to examine specimens in finer detail. As a result of this, the paleobotanist began to do his own field collecting, although a considerable selective element remained, for only the best preserved, the atypical, or the most conspicuous (usually the largest) specimens were collected. This museum-specimen concept still survives, and probably always will, but in the process of finding and collecting such a fossil, much valuable information is typically either disregarded or destroyed. Any paleoecological deductions based on specimens yielded by this selective collecting must necessarily be subject to the distortions inherent in the selective 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.

Only recently has there been a growing awareness of the need to investigate ways of extracting paleoecologically useful data from fossil deposits. A prerequisite of such an approach is the use of systematic sampling techniques and a change of emphasis from an analysis of the individual to an analysis of the population of fossils within an assemblage. The paleobotanist's traditional interest in anatomical and morphological detail for taxonomic and evolutionary schemes will continue to be critical because it is fundamental to the science.

No integrated study of the deposition of plant material with respect to the formation of megafossil assemblages has ever been carried out. Such a study will not only enable us to more accurately interpret paleovegetation and paleoclimates but also indicate where and how to sample plant remains so that more reliable stratigraphic work can be done.

Traditionally, such reconstructions of paleovegetation as have been attempted have been inferred by analogy with living vegetation with a focus on the ecological tolerance of supposed living relatives of extinct forms. Where the fossil record is considered incomplete, 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 paleoflora, 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 constituting a certain type of community have changed with time: that the floristic composition of communities has evolved as well as individual taxa. Clearly, if valid reconstructions of paleovegetation are to be made, then the criteria upon which such reconstructions are based should be as independent as possible of time-dependent biological variables and must be largely restricted to the physical and chemical processes that lead to the formation of a fossil assemblage. Little attention has been paid to the relations between fossil plant remains and their entombing matrix or those sedimentary characteristics that could furnish information on the depositional environment. Objective sampling of fossil remains and associated lithofacies may well provide a more stable basis for reconstruction of paleovegetation.

EARLY WORK

The first systematic paleobotanical sampling followed by a statistical analysis of the resulting data was carried out by Chaney (1924), although earlier attempts of quantitative sampling had been made by Davies (1908, 1920, 1921, 1929). Chaney investigated an allochthonous flora of Oligocene age in central Oregon, the Bridge Creek flora, and quantitatively compared the fossil assemblage with a modern redwood forest community that he considered to resemble the Oligocene vegetation.

The fossil deposit was sampled by excavating an area of rock some 4.5 m long and 1.2 m wide down to a depth of 0.3 m and splitting the excavated slabs parallel to the bedding in order to expose the fossil leaves, which were then counted. Further excavations were made at two other sites, and, in all, 2.65 m³ was excavated, yielding a total of 20,611 specimens. Even though he obtained this large sample size, Chaney believed that perhaps no more than 75 percent 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 paleoecological investigation. 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 a redwood forest were sampled using 0.3-m² quadrats, and leaf counts of the taxa occurring within these quadrats were then compared with the number of trees of those taxa growing within a radius of 15.2 m from each sampling station. Correlation values between the deposited leaves and the numbers of source plants were then calculated and these data used to estimate the number of source plants in the Bridge Creek forest that once grew within a radius of 15.2 m from the depositional site.

Unfortunately, this promising, though not flawless, (Wolfe, 1969) early work of Chaney was not until recently seriously followed up. Part of the reason for this was the lack of suitable statistical techniques with which to analyze the complexities of allochthonous assemblages where extensive predepositional sorting has taken place. Chaney did not investigate any floristic pattern that might have existed in the distribution of plant remains within the volume of rock he excavated but rather regarded each of the excavations as a single sample. Part of the aim of this paper is to show that patterns may exist, and that under certain circumstances they can be paleoecologically useful.

ANALYSIS OF QUANTITATIVE DATA

The development 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 similar statistical methods are frequently 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. The causal factors of patterns within a set of data cannot always be readily identified. In such complex situations Lambert and Dale reported (1964) "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."

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

semblages."

In plant ecology, there has arisen a dichotomy of approach to classification and ordination that has been the subject of extensive discussion in the literature (for example, Greig-Smith, 1964; Lambert and Dale, 1964).

Classification involves arranging stands, or observations, into groups, the members 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 applying classificatory techniques for the identification of lateral patterns within a single fossil assemblage is arguable.

The apparent distributional homogeneity of plant remains within a fossil plant assemblage is likely to be marked, owing to complex interaction of physical, chemical, and biological variables during transport, deposition, and diagenesis. Blackith and Reyment (1971) noted that sedimentary data contain a strong, apparently random element, and recent work by C. R. Hill (1974) has shown that large variation in species density between adjacent stands within an allochthonous plant bed is to be expected. The use of classificatory techniques where data are forced into discontinuous groupings under these circumstances may lead to highly erroneous results, particularly if incorrectly interpreted.

The alternative, multivariate ordination techniques, such as principal components analysis, does 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). A continuum is implied, but this does not preclude the existence of discontinuities within the sample population, and if these are present, they will be displayed by the technique.

The application of two ordination methods, principal components analysis (P.C.A.) and correspondence analysis (C.A) (M. O. Hill, 1974; called reciprocal averaging in M. O. Hill, 1973), will be tested on data relating to the deposition of plant remains in a recent sedimentary environment. From this, it is hoped that their suitability for detecting paleoecologically significant structure in data derived from allochthonous plant fossil populations can be assessed.

QUANTIFICATION IN PALYNOLOGICAL STUDIES

Although a quantitative approach has long been routine in the field of stratigraphic palynology, 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 paleoecology recognized that meaningful paleoecological conclusions could only be obtained if adequate information were 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 work was followed by a number of similar investigations of various depositional environments, some studies concentrating mainly on pollen deposition relative to sedimentation (see, for example, Traverse and Ginsberg, 1966), some on deposition relative to the source vegetation (see, for example, Peck, 1973).

It was soon realized that if reconstruction of past vegetational communities was ever to be achieved, generalized relations had to be derived linking the number of pollen grains of a particular taxon deposited to some measure of the abundance 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 Holocene depositional environment to the vegetational percentage of that species in the surrounding extant plant communities, fossil pollen percentages could be "corrected" to give an approximation of the species abundance in the ancient vegetation.

A number of serious flaws in the use of the R value have been discussed in the literature (Davis, 1969; Faegri, 1966). H. J. B. Birks (1973) stated that the most serious constraint 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; it is therefore impossible to accurately delimit the size of plot to be sampled in order to make valid comparisons between the fossil and modern source vegetation. Only in deposits within closed canopy forests or small basins can this problem be overcome (Andersen, 1970, 1973). Another variable is the structure of the source communities themselves; Janssen (1967) and Comanor (1968) have independently demonstrated significant variations in R values for the same tree taxa occurring in different forest types (H. J. B. Birks, 1973).

Provided that reasonably accurate data concerning differential productivity of the various taxa is available (Anderson, 1970, 1973), a more fundamental ap-

proach 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 wherein he 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 taxa deposited could, in theory, be determined and suitable allowances made when considering the reconstruction of paleocommunities.

Analysis of modern pollen dispersal and deposition has become more sophisticated and now constitutes a major branch of Quaternary studies. Multivariate statistical methods have also been used to analyze lateral distributions of pollen that (for example, O'Sullivan and Riley, 1974), and there is every reason to suppose that such studies will continue. Oldfield (1970) introduces a cautionary note: "Elegance of technique or consistency 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 MEGAFOSSIL STUDIES

Quantitative assessments of megafossil abundance have sometimes been used to supplement pollen data, as it is generally considered that megafossils represent only the local components of the flora.

The most notable of such studies was carried out by Watts and Winter (1966), who examined the megafossil content of cores taken for pollen analysis from Kirchner Marsh, Minn. The results were presented in the form of seed diagrams similar to those traditionally used for displaying the pollen spectrum. These workers found that many of the concepts of pollen analysis could be equally well applied to seed analysis, although they pointed 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 critical for both stratigraphic and paleoecological studies, for conclusions based on a restricted sample from only a small number of cores could lead to erroneous conclusions. Yet, this heterogeneity in the megafossil distribution (not only with seeds but also leaves and other remains) may well prove to be the strong point of megafossil 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 relation of the various sources. This, to a large extent, is not the case with the dispersal of macroscopic remains.

The application of multivariate statistical techniques to the analysis of megafossil distributions, as in pollen studies, 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. A known volume of sediment, usually 50 cm³, was then analyzed for its megafossil content, and the numbers of each taxon were expressed as numbers per 100 cm³ of sediment. Megafossil and vegetational data were then analyzed using correspondence analysis (referred to in Birks' paper by its French title "Analyse factorielle des correspondences"); the resulting ordinations showed a direct relation between the megafossil content of the lake bottom muds and the surrounding vegetation. The pattern of megafossil distributions within the lakes was observed; most species were concentrated close to the shoreline.

The distribution of megaremain (including leaves) in a lake environment was investigated by McQueen (1969) at nine stations in and around a New Zealand lake. From simple tabulation of the data, McQueen concluded that in lake sediments the plant remains represent only the dominant members of the surrounding vegetation, as no remains were found that had been transported any appreciable distance. In unimpeded rivers, however, remains may be carried considerable distances and still be recognizable. For instance, it was concluded that a leaf of *Nothofagus menziessii* Oerst. from a swamp site bordering the lake must have traveled at least 2 km downstream; 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 megafossil assemblages has also come from paleobotanists working on specific fossil plant assemblages. Observations by Mosely (1892) on plant debris transported out to sea by the River Ambernoh in New Guinea were quoted by Reid and Chandler (1933), who proposed a similar mechanism to explain the occurrence of leaves, fruits, and seeds in the London Clay. 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 in which leaf discs were rolled together with water and sand, it was concluded that abrasion alone was unlikely to cause serious destruction of fresh material.

C. R. Hill (1974) investigated the practicability of quantitatively sampling fossil plant remains of the Yorkshire Jurassic flora exposed at Hasty Bank. Three vertical sections of the deposit were recovered by excavating known volume of rocks, and recovery of the

plant material was achieved by careful splitting along the bedding planes. Contiguous samples were taken from top to bottom of the sections that cut across two lithologies, a siltstone and a mudstone. In one section, accurate counts were made of the number of plant fragments of the different species that were recovered as well as visual assessments of abundance using a pseudologarithmic scale of 1–10. In the other two sections, only the visual abundance estimate was used. Hill presented his data in histogram form, from which he was able to conclude that there were a number of different assemblages present within the rock that he sampled.

Part of Hill's data was then analyzed using both principal components analysis (P.C.A.) and correspondence analysis (C.A.) (Spicer and Hill, 1979). Using C.A., all assemblages identified by Hill could be detected but only when the count data were either logarithmically transformed or reduced to an arbitrary pseudologarithmic scale. When data from a group such as the Bennettiales (*Cycadeoides*) was ordinated, C.A. was able to detect associations between the vegetative and reproductive parts of fragmented plants. It was known from other evidence that the detached organs so grouped did in fact represent parts of the same type of plants.

R. Pfeiffer (oral commun., 1974) has investigated the lateral variation in plant distributions in shales above coal seams exposed in Indiana strip mines. As mining operations proceeded, 0.3-m³ samples were cut from the rock by means of a chain saw, and analysis of the species content of the samples made in the laboratory.

Scott (1977, 1978) has attempted to investigate the distribution of Pennsylvania plants in roof shales using quantitative estimates of "cover."

KRASILOV'S CLASSIFICATION OF PALEOSUCCESSIONS

Krasilov (1969) proposed a scheme of classification of plant-fossil deposits based on those processes supposed to have determined 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." Krasilov then asserted that it is necessary to distinguish between changes due to real successions of the ancient vegetation and changes due to transport and burial.

Krasilov's classification of paleosuccessions can be summarized in this way:

Taphogenic paleosuccessions—resulting from the

selective characters of burial, transportability, and strength of plant remains.

1. Selective taphogenic—resulting from sorting during transport.

2. Lithification paleosuccessions—resulting from changes in the composition of the buried vegetation assemblage in the course of diagenesis.

Cenogenic paleosuccessions—produced by the evolution and migration of floras.

1. Mutational cenogenic—as yet to be recognized in the field but formed by the alteration of vegetation brought about by genetic changes.

2. Phenological—expression of seasonal variations.

3. Migrational—brought about by the migration of floras due to:

Topogenic factors—change in topography and relief.

Edaphogenic factors—changes in the soil characteristics.

Climatogenic factors—climatic changes.

While such a classification has its uses, its rigid application invites oversimplification of the processes involved in determining the species composition of an assemblage. More than one type of paleosuccession 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 presented in the section "A General Model of Leaf Deposition in a Fluvio-lacustrine Environment" is just such a situation where, at deposition, taphogenic and topographic/edaphic paleosuccessions merge laterally, whereas subsequent diagenetic changes introduce the possibility of a lithification paleosuccession being formed. Such a classification may be useful when describing large-scale depositional regimes, but its application to individual deposits is undocumented and may prove to be of doubtful value.

This background to the present study portrays many workers experimentally investigating isolated aspects of sorting and deposition as an aid to interpreting fossil assemblages. The deposition of plant megaremaines is, however, a process that involves many variables and cannot be understood unless an integrated study of the various interrelated aspects is made. The quantitative analysis of fossil plant assemblages to give paleoecologically significant information is clearly in its infancy. Before going too far forward, particularly in the development and application of sophisticated numerical techniques, it is necessary to ask some basic questions: 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? How can we obtain

the most objective and efficient sampling of a fossil deposit?

Answers to these and similar questions involve a wide range of considerations from the measurement of extant vegetation, the mechanics of transport and deposition, through the fossilization process to the sampling of the fossil population and subsequent mathematical analysis. The aims of this paper, then, are to evaluate the effect on paleoecological information of these processes using a small modern fluviolacustrine depositional environment as a working system, to erect a generalized model of deposition of megaremaines in such an environment, and to show how existing mathematical techniques can be used to reveal significant patterns of distribution of deposited plant remains.

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FIELD SITE

The modern depositional environment chosen for this study was an actively advancing freshwater lacustrine delta in the grounds of the Imperial College Field Station at Silwood Park (Grid ref. SU 941691), Berkshire, England. Rocques' Survey of Berkshire (1761) (Berkshire County Records office) 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 (Berkshire County Records office), shows a lake, much larger in extent than at present, extending southwestward as far as Cascade Bridge (fig. 1); on a geologic map of 1819 by William Smith (Imperial College Geology Department, London), no lake is shown. It is likely that an existing, possibly slightly out-of-date, map was used as the base for the geologic map; the date of the construction of the lake may be

reasonably supposed to have been just prior to 1815.

Silwood Lake was artificially constructed by damming the northeastern end of the existing valley. It was thought that the lake had been "puddled" to prevent drainage through 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 base of the surrounding hills indicates that the water table in the Bagshot sands is locally higher than the water level in the lake, 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 most of the southwestern arm of the lake has since filled with sediment brought down by the stream (fig. 1). The present delta front, approximately 300 m northeast from Cascade Bridge, is some 60 m or so wide. If the average sediment depth is 2 m, then the approximately 18,000 m³ of sediment has been deposited since about 1800, an average rate of 100 m³ per year. Although no accurate measurements were made, the delta was seen to be actively laterally advancing at the rate of about 1.0 m per year during the course of this study. Most of this delta deposit now supports a mature *Alnus glutinosa* (L.) Gaertn. thicket (figs. 2 and 3).

The existing weir was constructed in 1958 and now maintains the lake level constant to within a few centimeters; during construction of the weir, the lake was partially drained for some time.

It is known that the stream supplying sediment to the southwest arm of the lake has been artificially straightened (E. Green, Imperial College, oral commun., 1974), although no accurate date for this event is available. It appears that before this construction, the stream emptied into the lake to the south of its present inflow, 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 breaches the partly natural levees along the terminal 300 m of its extent, resulting in periodic flooding of large areas of the compacting delta sediment. No accurate streamflow data are available, but during the course of our observation, the flow rate rarely exceeded 1.0 meter per second.

Silwood Lake, small by comparison with many freshwater bodies (surface area approximately 13,000 m²), is about the same size as many fossil-leaf deposits: for example, the Tennessee clay pits described by Dilcher (1971) and the Kreuzau deposits described by Ferguson (1971). Both of these deposits are supposed to have been laid down in an oxbow type of lake. Such an environment may well be conducive to the fine preservation exhibited by fossils from both localities. Unfortunately, it is unlikely that this type of deposit will yield significant information concerning distant vege-

tation, because 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 an environment similar to that of the Silwood environment. These lakes form when sediments of a large river are deposited as levees and back

up water in a tributary stream. 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 basin (Hutchinson, 1957). The deposits of such lakes may well yield fossil leaves derived from both riparian and slope vegetation. Despite the artificial nature of the Silwood lake and the present stream course, natural processes of transport and sedimentation are considered to be operating.

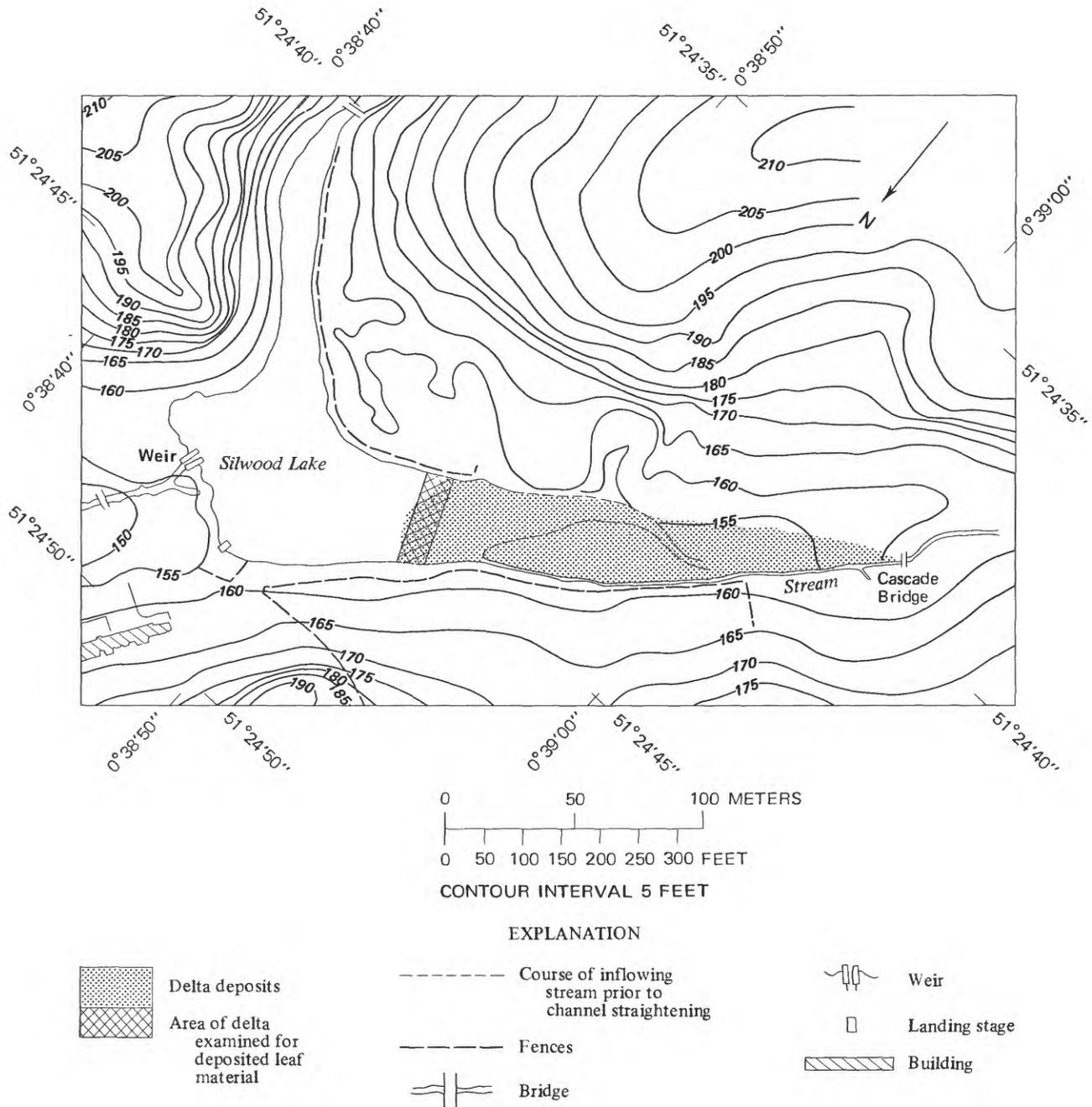


FIGURE 1.—Silwood Lake and immediate area showing extent of deltaic deposits.

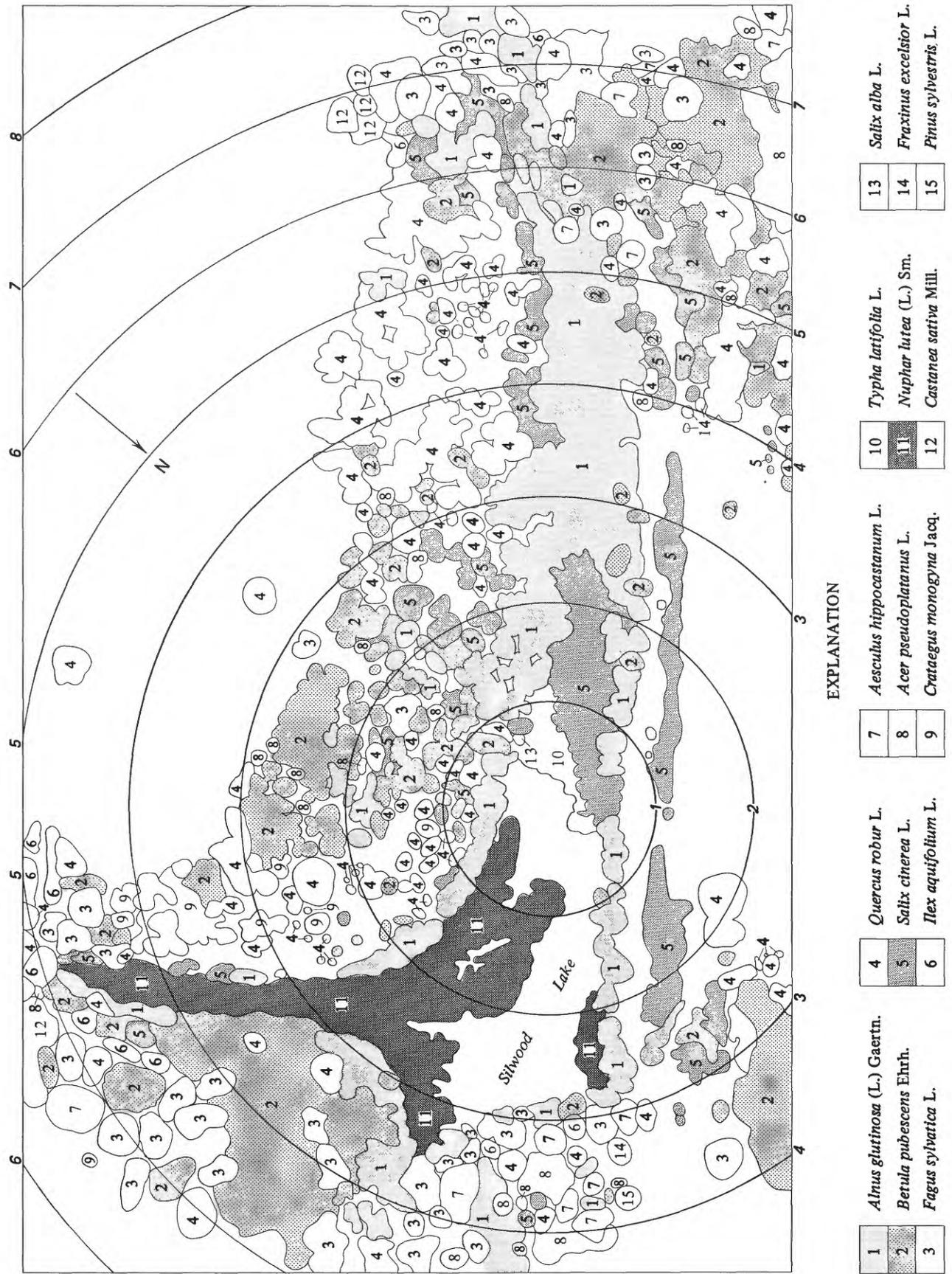


FIGURE 2.—Distribution of tree species constituting the canopy around Silwood Lake, as seen from the air. Except where the canopy is continuous, approximate sizes of the crowns are indicated.

MATERIALS AND METHODS

ANALYSIS OF VEGETATION SURROUNDING SILWOOD LAKE

It is clear from the literature (see, for example, Newbould, 1967; Hughes, 1971) that to obtain a representative estimate of the total litter produced by an area of vegetation as extensive as that surrounding Silwood Lake would be a major task and take a number of years. To undertake such a project in the course of this study was not feasible, but it was possible to map the position of every tree species that constitutes 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 September 8, 1971, was used as the basis for a vegetation map, and the species of every tree seen from the air then determined and plotted by ground survey (fig. 2).



FIGURE 3.—Stream flowing toward Silwood Lake as viewed from Cascade Bridge.

The vegetation map was divided into regions of interest at various distances from the delta 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 center and measuring (using a 1-mm 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 progressively summed and successive percentage areas for the species within the complete circles of increasing radii calculated. The percentage species composition for the 400-m-radius circle was taken as representative of a summary of the vegetation in the field area. The results are shown in table 1.

DELTA LEAF TRAPS

To determine the proportions of leaves of the various species deposited on the delta surface by direct wind transport, 15 water-filled leaf traps were positioned on the delta (fig. 4). The trap frames (fig. 5) were constructed of wood covered with a polyethylene sheet ("1,000" grade) pinned to form a 0.5-m² shallow water-tight tray 5 cm deep. A small hole was 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. 4) 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 percent aqueous formaldehyde until such time as they could be counted. The water level in the traps was topped up as required.

Leaf traps of similar design were 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 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. Because of this problem, the experiment to estimate litter input to the stream was abandoned, but some of the leaves collected in undisturbed traps were retained for size comparison with the lake samples.

The numbers of leaves of different species falling into the delta traps were determined and the results given in table 2. The areas of *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

TABLE 1.—Percentage crown cover of trees occurring within circular areas of increasing radius centered upon the delta, Silwood Lake

Circle No.	Radius (m)	<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Salix cinerea</i>	<i>Salix Alba</i>	<i>Ilex</i>	<i>Aesculus</i>	<i>Crataegus</i>	<i>Acer</i>	<i>Fraxinus</i>	<i>Castanea</i>
Percent total area													
1	50	51	8	---	9	32	1	---	---	---	---	---	---
2	100	34	18	2	13	32	---	---	---	1	---	---	---
3	150	25	34	3	10	24	---	---	1	2	1	---	---
4	200	24	34	6	20	5	---	---	4	4	4	1	---
5	250	18	25	17	26	6	---	3	2	---	3	1	---
6	300	12	28	9	27	8	---	3	8	2	2	---	5
7	350	11	51	3	17	15	---	2	---	---	---	---	1
8	400	8	18	31	22	---	---	---	6	---	9	---	6
Cumulative percent													
1	50	51	8	---	9	32	1	---	---	---	---	---	---
2	100	37	16	2	13	32	---	---	---	1	---	---	---
3	150	30	26	3	11	27	---	---	1	1	1	---	---
4	200	28	30	4	15	18	---	---	2	2	2	1	---
5	250	25	28	7	17	15	---	1	1	2	2	1	---
6	300	23	28	7	19	14	---	1	2	1	2	1	1
7	350	22	31	7	18	14	---	1	2	2	2	---	1
8	400	21	28	9	19	13	---	1	2	2	2	---	1

results are presented by histogram, figures 19 and 20, and tested using a Fisher-Behrens test (as described in Campbell, 1967).

WIND DIRECTION AND SPEED

Surface-wind direction and strength for July to December 1973, as measured at Heathrow Airport (12.9 km northeast of Silwood Lake), were obtained from the British Daily Weather Reports. Although local topography may slightly modify the wind patterns around the lake, it was assumed that these readings would serve as an estimate of the wind conditions at Silwood Park. The wind direction and speed was recorded four times in every 24 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 calculated (fig. 18). Weighting by wind speed was employed because it may be argued that a strong wind exerts more influence on wind dispersal than a gentle breeze. No corrections were made for periods of rain that could have reduced wind dispersal. The weighted wind-direction data was processed using the program ORIPAL as published in Reymont (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 taken and put into buckets that were three-quarters full of chlorinated tap water. At various times during the course of the experiment, the leaves

were stirred round in the water and left to settle; the number that remained floating were counted. It was soon realized that with those species where most leaves sank within 2 days, large errors were incurred by not having any readings during the night. To overcome this problem, a light-plane recording apparatus (diagrammatically shown in fig. 6) was constructed.

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

To compensate for any discoloration 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 light cell receiving this reference beam was electronically balanced with the cell receiving the light plane.

It was noted that unless the leaves were intermittently agitated, they were prevented from sinking, even though they were waterlogged, by the formation of gas bubbles on the external epidermal surfaces. A mechanical agitator was therefore constructed to periodically generate ripples on the surface of the water. In practice it was found that even minimal agitation of the water cause previously sunken leaves, with a buoyancy only slightly in excess of neutral, to be

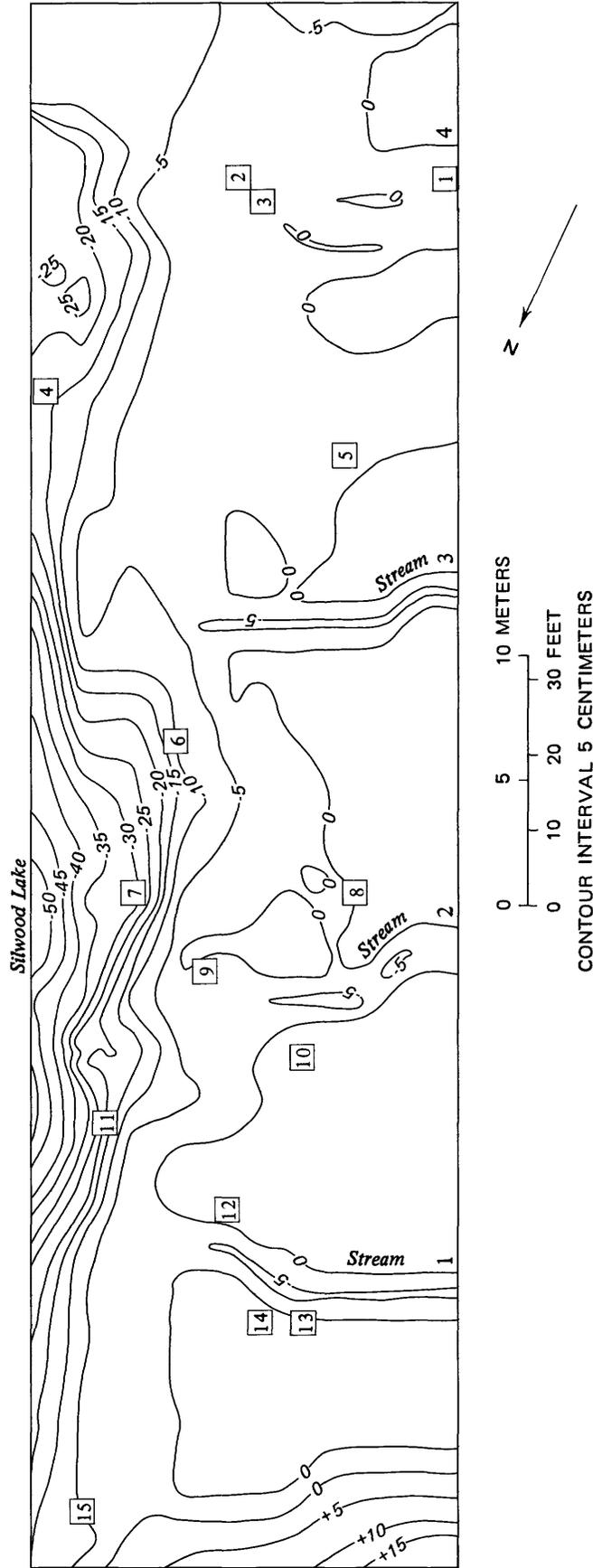


FIGURE 4.—Locations of leaf traps on a contour map of delta surface. Distributaries are numbered 1 through 4. Relative importance of distributaries visually assessed, expressed in terms of percentage of total stream flow during period of sampling. Distributary 1: 50 percent; 2: 30 percent; 3: 20 percent. Distributary 4 was not directly connected to the inflow stream and seepage from the south bank. Contour map was hand drawn from a regular bathymetric matrix.

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 this remains to be tested.

LEAF-DEGRADATION EXPERIMENTS

The relative degradation rates of leaves of *Quercus robur* L., *Fagus sylvatica* L., *Betula pubescens* Ehrh., *Salix cinerea* L., and *Alnus glutinosa* (L.) Gaertn. were investigated by the following experiments.

Three hundred and sixty freshly fallen intact leaves of *Quercus*, *Fagus*, *Salix*, *Betula*, and *Alnus* trees, all 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. Seventy-five

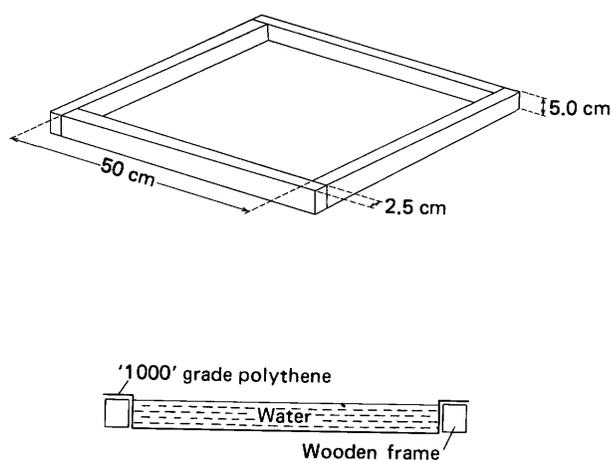


FIGURE 5.—Construction of leaf traps. Wooden frame constructed to dimensions shown and lined with polythene sheet. Shallow tray so formed is filled with water. Buoyancy of wooden frame insures that even when trap is positioned in open water, edges are clear of water, preventing leaf exchange in and out of trap.

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

Trap No. (fig 48)	<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Salix cinerea</i>	<i>Nuphar</i>
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	1 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	---	---
Total	542	42	24	47	31	2
Percent total	79	6	3	7	5	---

¹Probably transported by water fowl since both pieces bore beak marks and the trap was apparently undisturbed.

leaves of each of the taxa were placed in each of four rectangular nylon cages (25 × 25 × 6.5 cm) constructed of 5-mm² mesh Netlon. No metal was used in the construction, and all seams were made using nylon thread. Two cages were weighted (with iron ballast sealed in a "1,000"-gauge polythene bag so that the leaves could not be contaminated by the ballast) and deposited on the bottom of the lake, and two cages were tied to a wooden stake in the stream that had not been 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, the remaining samples from the other.

Five leaves of each species were taken for X-ray microanalysis (a full account of the X-ray microanalysis studies, which are not discussed here, is given in Spicer, 1975), the remaining 20 leaves used for leaf-degradation studies. The leaves were carefully washed to remove loose sediment and the extent of natural leaf degradation recorded, either by photocopying 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 as to afford free access to most aquatic invertebrates, yet retain all but the smallest leaf fragments. The degree of breakdown of the various species is shown in figures 27-36.

The washed leaves were loaded into the drum of a rolling apparatus (described below) together with 2.5 liters of tap water and rolled for 90 minutes. From preliminary experiments, using both fresh leaves and leaves collected from the streambed, it was found that in this treatment fresh leaves were only minimally damaged, whereas 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 periods were rolled together; the last three could only be treated separately because a large number of fragments were generated and subsequent identification of the fragments became extremely tedious. The resulting fragments were then stored in 5-percent aqueous formaldehyde solution until such time as they could be counted and, in some cases, their areas determined using a Paton electronic planimeter. Because a drop in accuracy was found when measuring large number of small areas, only the areas of fragments from the leaves receiving the shortest exposure to the lake or stream environments were measured.

ROLLING APPARATUS

The rolling apparatus (fig. 7) consisted of a plastic drum 22 cm in diameter and 36 cm long with a 1.2-cm-thick removable transparent plastic ends. The drum was fitted with cylindrical wooden paddles as shown in the diagram and supported on two rubber-clad rollers (external diameter 17 mm), one driven at constant speed by a ¼-horsepower electric motor. The drum rotated at a rate of 70 revolutions per minute. A water-tight seal between the drum and the end plates was achieved using "Sealastic" sealing compound.

The wooden paddles provided 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 that it would expose the leaves to some of the forces likely to be found in nature. The water energies acting on the leaves within the drum were fairly high, but this insured that fragmentation was as rapid as possible and that the effect of continued, indeed accelerated, microbiological activity under the relatively warm laboratory conditions was minimized during the rolling period.

The frequency distributions of the various fragment areas produced by rolling were plotted as histograms, (figs. 37–39). At first it was 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. Examination of the histograms (figs. 37–39) reveals that the distributions are in fact bimodal. It appears that the peak at low size

classes represents large numbers of small fragments 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 shown by the figures 40–43.

LEAF DISTRIBUTIONS IN THE DELTA SURFACE SEDIMENT

The lateral distribution patterns of leaves deposited 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 strings 2 m apart, each marked off into 2-m lengths. In this way accurate sample location was achieved. Access to the delta was by a flat-bottomed dinghy, from which samples were collected. Water depths were measured using a weighted measuring tape and the water-depth data used to draw a contour map (figs. 4, 8, 57, 62) of the delta surface.

Samples of the leaves entombed in known volumes of sediment were taken at the positions indicated in figure 8. Species/area curves were constructed using rectangular wire quadrats, and from this data a sample area of 0.5 m × 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 apparatus shown in figure 9. A sheet-metal frame (A) was constructed 0.5 m square with external lateral "wings" (5 cm wide)

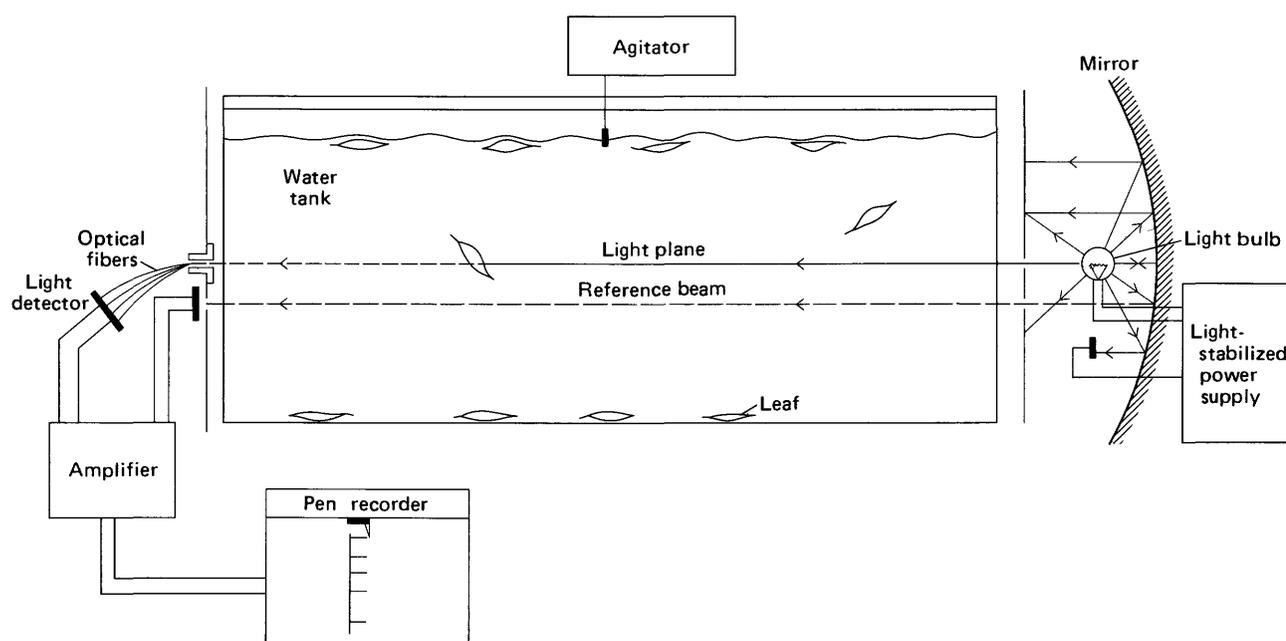


FIGURE 6.—Diagram of light-plane apparatus for recording leaf-sinking events. See text for explanation. Tank is approximately 1 m long.

that prevented its sinking into the sediment during sampling. Two centimeters below these wings, on the inside of the frame, were two ledges along which the cutting edge of the sieve quadrat (*B*) could be pushed. 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 $0.5 \times 0.5 \times 0.02$ m was retained on the sieve quadrat. The sediment was then carefully washed through the sieve (0.5-cm² mesh), which retained the larger plant remains. These remains were then removed from the sieve, returned to the laboratory in polythene bags, and stored in 5-percent aqueous formaldehyde until needed for examination.

ANALYSIS OF LEAF REMAINS

The leaf remains, washed free of formaldehyde solution, were separated into whole leaves and fragments. A leaf was considered to be whole if it was thought to have at least 80 percent of the area of its lamina present and not less than 80 percent 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 cm² using a gridded perspex overlay. If any fragment proved difficult to identify, the cuticle was prepared by oxidizing the tissues in 20-percent aqueous chromium trioxide for 12 hours at room temperature. The cuticle was washed with water, stained in 1-percent aqueous safranin, and

mounted in glycerine jelly before being identified by comparison with a reference collection of cuticles. The resulting data were subsequently analyzed using multivariate statistical techniques.

CORING PROCEDURE

The three-dimensional nature of the Silwood deposit was investigated by taking 22 cores, each 7.5 cm in diameter, in the positions shown in figure 10. The corer used was modified from the design published by Livingstone (1955). Various workers 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 apparatus described here utilizes a flexible polythene liner to facilitate removal of the core from the core barrel.

A 2-m length of plastic pipe served as the core barrel. This material, 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 tubular "1,000"-grade polythene liner was tassellated, bent back over the end of the core barrel, and taped to the external surface of the plastic pipe below the brass ferrule. A brass cutting head screwed onto the ferrule so that an internal brass lip closed onto the end of the liner and pipe, forming a flush seal (fig. 11). The cutting surface of the bit was serrated to aid in penetrat-

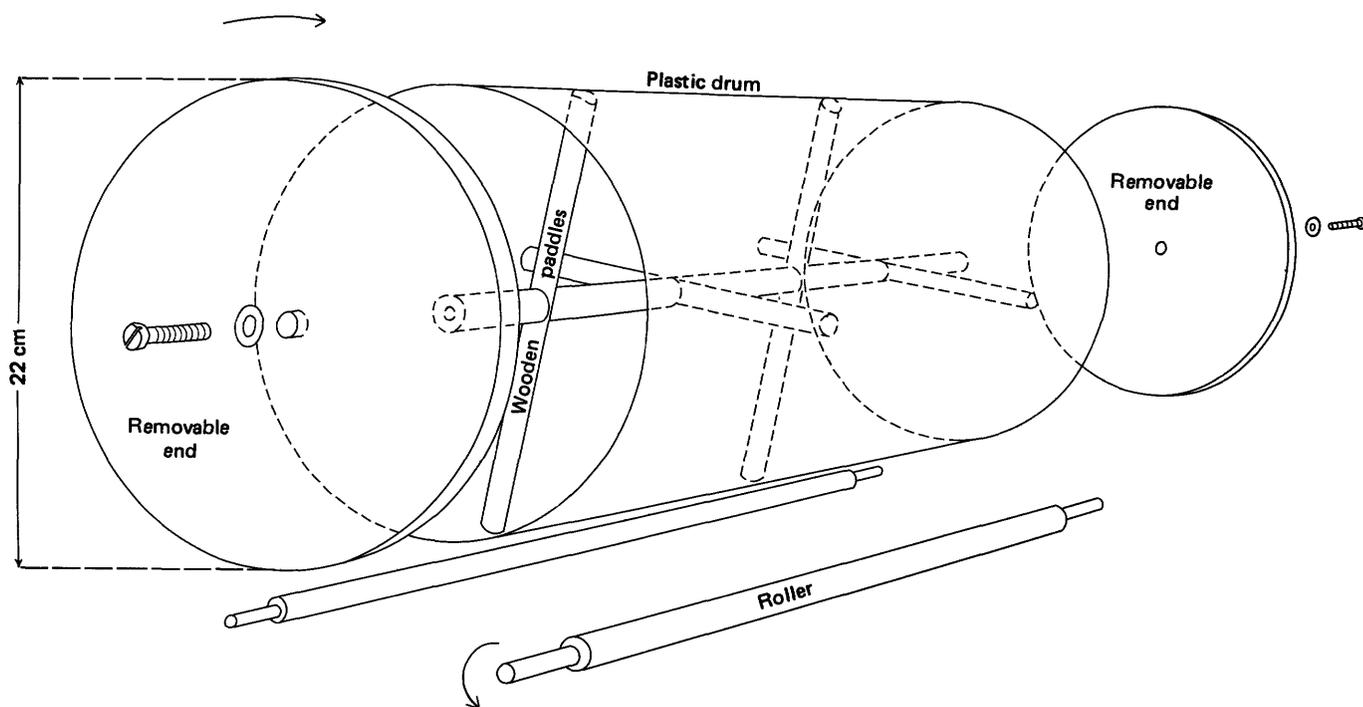


FIGURE 7.—Diagram of the leaf-rolling apparatus (36 cm long). See text for explanation.

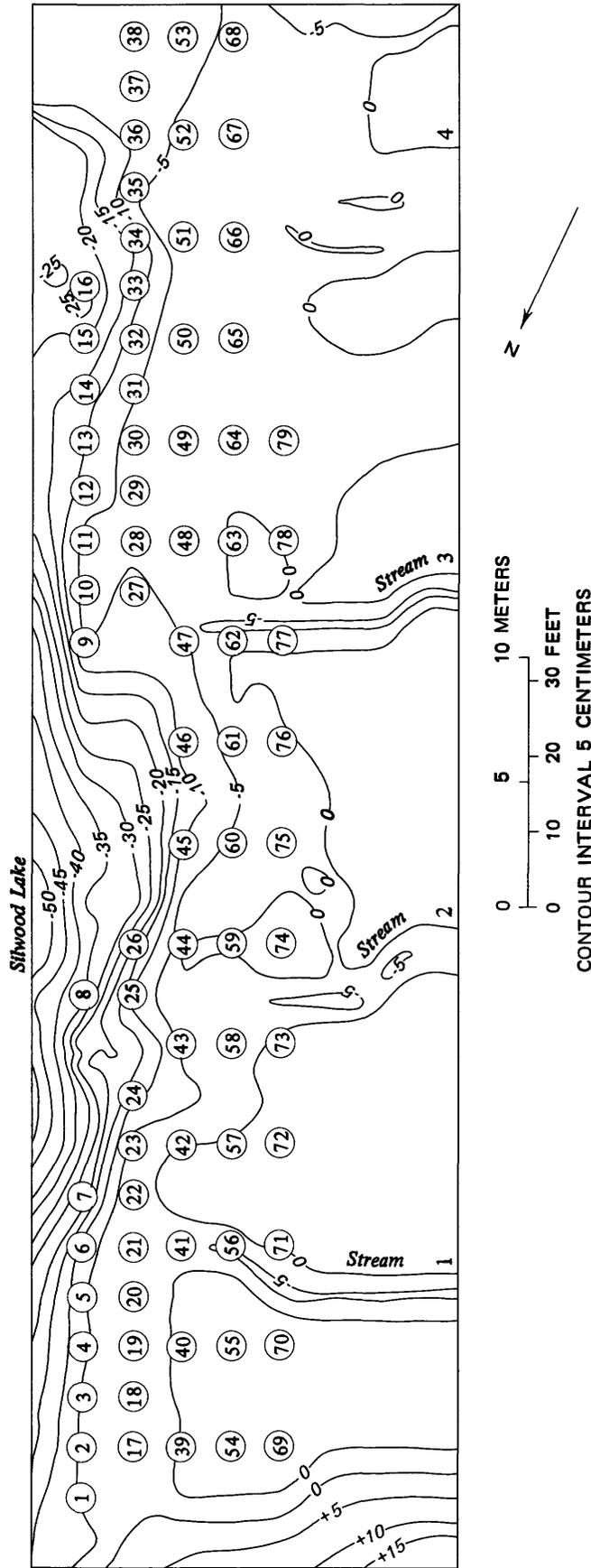


FIGURE 8.—Position of leaf samples collected from surface sediment of delta using sampling frame shown in figure 9. (Same base as fig. 4) Quadrats are numbered.

ing organic debris.

To facilitate safe working on the delta, a floating drilling "rig" was constructed (fig. 12). After positioning the rig on the sediment, the core barrel, with its previously inserted liner, and bit were assembled. The operation of the corer is similar to that described by Livingstone (1955). The rubber piston (fig. 11) was positioned at the cutting edge of the bit. The piston was then held stationary relative to, and in contact with, the sediment surface by means of a rope that passed over a pulley at the top of the rig. The core barrel was 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 returned to the laboratory before being examined. In this way, not less than 95 percent 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. This part of the procedure is fundamentally different from the piston extrusion method described by Livingstone. When numerous gas vesicles are present within an unconsolidated core, his procedure may introduce what may be termed "secondary compaction" during the extrusion process. By extracting the core within the liner, this problem was avoided. After the core was exposed by cutting the liner with a razor

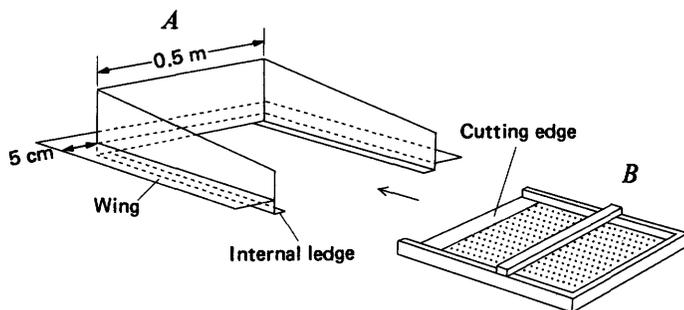


FIGURE 9.—Sampling frame for collecting leaf samples from delta surface sediments. Frame A was positioned in sediment such that "wings" were level with sediment surface. Sieve quadrat B fits into frame A so that cutting edge runs along internal ledge of A. When B is lifted out of A, sediment is carefully washed through sieve; retained leaves are removed for laboratory analysis.

blade, a full description of the core was made and samples of sediment were 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 removed for further study. No attempt was made to quantitatively sample the leaf concentrations within the core sections; the leaves and fragments were carefully removed from the sediment by washing, and a subjective examination was undertaken.

Eh and pH measurements were made 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 in which holes were cut, and the pH/Eh electrode was rapidly inserted into the sediment. The results are shown in table 5.

Sediment samples, approximately 10 g each, were taken at 0.2-m depth intervals and weighed in aluminum boats of known weight. The sediment was then dried at 80°C to constant weight. The dried sediment

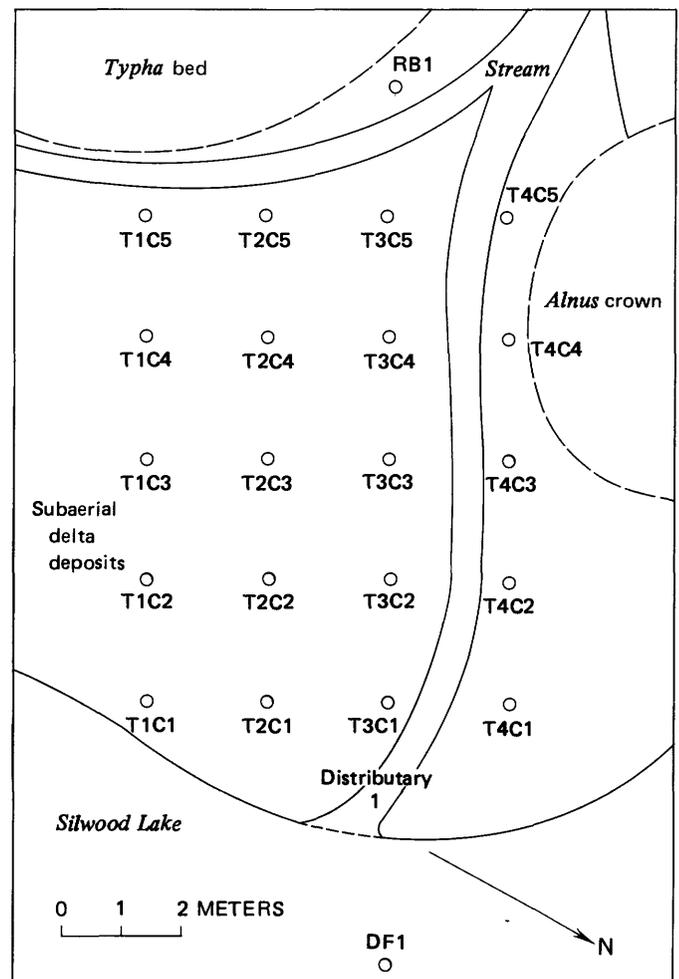


FIGURE 10.—Position of cores relative to delta. (See figs. 44 and 45 for diagrams of cores.)

was subsequently digested in concentrated nitric acid and the iron content of the digests measured using atomic absorption spectrophotometry. After obtaining the iron content of the sediment, the weight loss on drying was 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 5.

VEGETATION ANALYSIS

Before attempting any comparison between a depos-

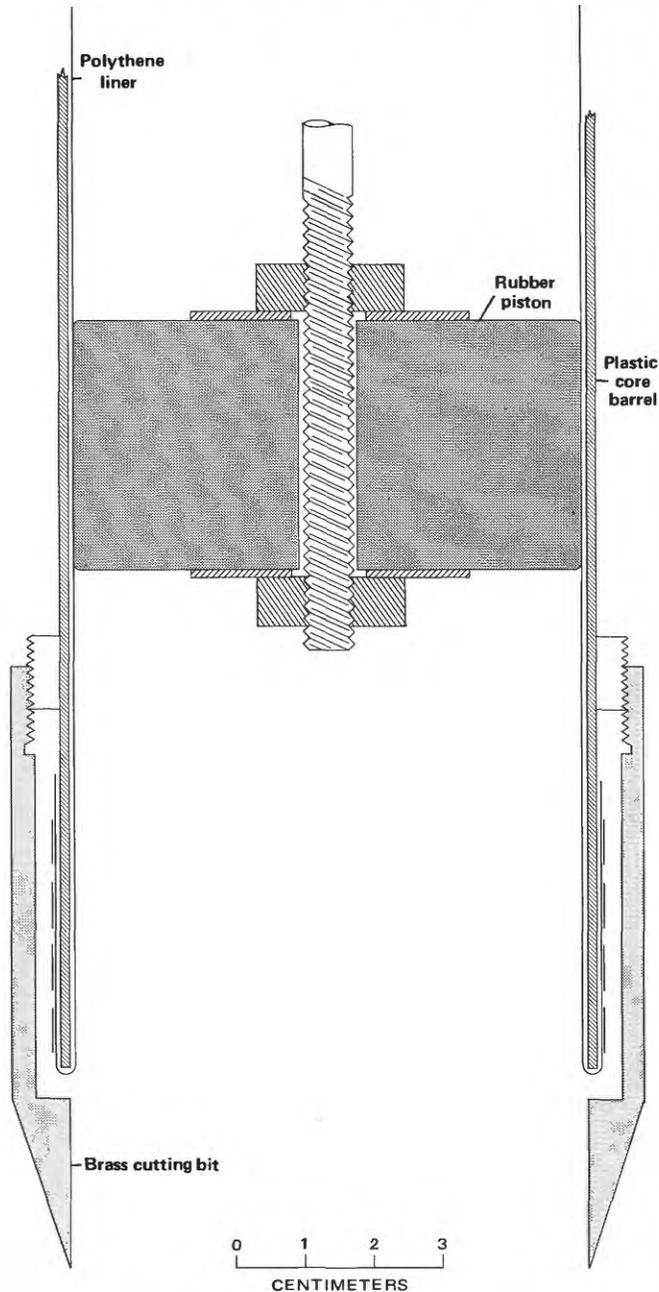


FIGURE 11.—Corer assembly. See text for description.

ited 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, each community displaying a greater degree of homogeneity within itself than is exhibited in the whole. In natural vegetation, boundaries between communities are rarely well defined, however, and ecotones may occupy areas larger in extent than the communities themselves. Yet 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 then tends to be regarded as a distinct pollen source. As delimiting these vegetational areas has usually been a subjective process, the actual parameters likely to control pollen production have not been recorded.

Although it is dangerous to oversimplify vegetation into "blocked" source areas, such a concept is useful



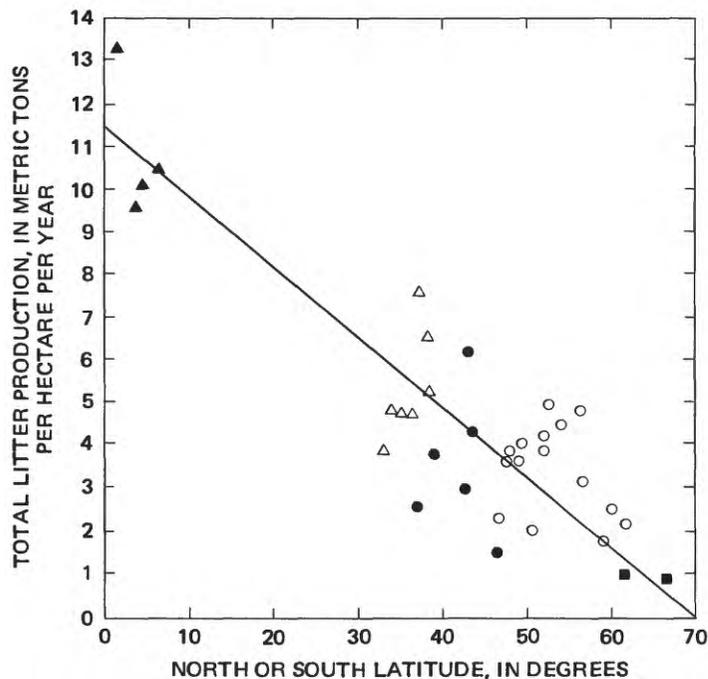
FIGURE 12.—Coring delta deposit. Unconsolidated nature of sediment allowed core barrel to be driven by hand. For full description of coring procedure, see text.

when attempting to reconstruct ancient vegetation. 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.

In megafossil analysis, factors affecting the litter production by the vegetation are critical because a megafossil assemblage may be thought of as a distorted sample of the capacity of the vegetation to produce leaves, fruits, seeds, or other organs. 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 parameters may be summarized and discussed as follows, bearing in mind that the observations refer to the dry weight of material, not the number of leaves, fruits, and seeds.

NATURE OF THE TREES

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



EXPLANATION

- | | |
|---------------------------------|---------------------------|
| ▲ Equatorial | ○ European cool temperate |
| △ Warm temperate | ■ Arctic/Alpine |
| ● North American cool temperate | |

FIGURE 13.—Annual total forest litter production in relation to latitude. After Bray and Gorham, 1964.

ENVIRONMENT

CLIMATE

The effect of latitude on litter is plotted in figure 13. If such a pattern existed in the past, it is not surprising to find that many fossil assemblages represent tropical, subtropical, or warm temperate floras, even allowing for high rates of biological degradation. The relevance of the plot (fig.13) to the litter production of ancient vegetation systems is 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 relation may be radically affected by climatic conditions, which are known to have varied markedly in the past.

ALTITUDE AND EXPOSURE

Bray and Gorham suggest that in mountainous areas, rainfall and temperature tend to be optimum for forest growth at intermediate elevations; the evidence presented is not conclusive. They imply that litter production would be at a maximum under these conditions. As the chances that a mountain flora will be preserved in the geologic record are small, effects of this kind on litter production are of limited interest to the paleoecologist. 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 litter production tends to decrease 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 mainly concerned with the effects of major changes in soil type, but minor soil differences could significantly affect litter production and hence the likelihood of some species being represented in the fossil record.

TREE DENSITY

There is no evidence to suggest that tree litter is affected by the density of individuals, provided the canopy is complete. But there does appear to be a distinct correlation between the annual fall of litter and stand basal area in both gymnosperms and angiosperms. In this respect, Bray and Gorham quote the work of Bonnevie-Svendson and Gjems (1957). It appears that quantitative analysis of closed-canopy vegetation using tree-density measures may give rise to misleading community classifications with respect to any derived megafossil assemblages.

TIME

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 with slight variations due to such climatic fluctuations as wet and dry seasons. In temperate latitudes, most species show a peak in litter production at certain times of the year, most coinciding in the fall.

The total litter fall may differ greatly from year to year; if any useful litter estimates are to be achieved, measurements must be taken over a period of several years. Although, as stated, such a study is necessary outside the scope of this present work, litter falling directly onto 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 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. Note, however, that major components of the source vegetation, namely, the herbaceous plants of the understory, 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 vegetation such 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, defined as the proportion of ground occupines by a perpendicular projection onto 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 cover would be difficult on the scale required.

The measurement of crown cover, that is, the measurement of the area of horizontal ground surface occupied by a vertical projection onto it of the crown of a tree, was adopted as a compromise that offered a rapid estimate of species abundance that was somewhat related to litter productivity. The only part 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 winds sufficient to transport them significant horizontal distances. In the Silwood environment the only place where the greater part of the total litter production from a group of trees could form the input to a depositional environment is at the streamside or lakeside. Leaves falling into the stream water are likely to represent a mostly unbiased sample of the woodland litter.

If, however, the stream is of such width that the canopy is broken, the resulting increase in light intensity along the stream course will stimulate the growth of streamside understory plants. Such a phenomenon is clearly seen in riverside vegetation in tropical rain forests (Richards, 1966) and is common around lake margins. Under such conditions, the taxa represented in the litter fall into a stream or lake will not be repre-

TABLE 3.—Summary statistics of the plant remains collected from within the top 2 cm of delta sediment at the positions shown in figure 8

	<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Salix cinerea</i>	<i>Ilex</i>	<i>Aesculus</i>	<i>Acer</i>	<i>Crataegus</i>	<i>Typha</i>	<i>Nuphar</i>	<i>Salix, Alba</i>	Totals
Number of fragments	1,315	272	320	559	482	165	23	7	4	185	31	20	3,383
Number of whole leaves	722	187	175	69	413	5	9	----	4	----	----	14	1,598
Total number of remains ¹	2,037	459	495	628	895	170	32	7	8	185	31	34	4,981
Fragments/Whole leaves (number)	1.82	1.45	1.83	8.10	1.17	33.00	2.56	----	1.00	----	----	1.43	2.12
Fragments/Total (percent)	65	59	65	89	54	97	59	100	50	100	100	59	68
Total fragment area ²	7,561.5	623.5	768.5	826.5	882.0	218.0	232.5	10.5	10.0	321.5	235.0	84.5	11,774
Total whole-leaf area ²	11,573.5	1,317.0	2,181.5	1,053.0	1,800.5	30.5	309.5	----	15.0	----	----	143.5	18,424
Total area ²	19,135.0	1,940.5	2,950.0	1,879.5	2,682.5	248.5	542.0	10.5	25.0	321.5	235.0	228.0	30,198
Percent fragments/Percent whole leaves (area)	65	47	35	78	49	715	75	----	67	----	----	59	64
Percent fragments/Percent total (area)	40	32	26	44	33	88	43	100	40	100	100	37	39
Mean whole-leaf area ²	15.94	8.10	12.39	15.40	4.36	6.10	25.79	----	3.75	----	----	10.25	----
Standard deviation whole-leaf area	10.27	10.21	6.52	8.78	4.37	4.08	20.71	----	3.01	----	----	5.38	----
Mean fragment area ²	5.75	2.29	2.40	1.48	1.83	1.32	10.11	1.50	2.50	1.74	7.58	4.23	----
Percent total number of whole-leaves	45	11	11	4	26	1	1	----	1	----	----	1	----
Percent total number of remains	41	9	10	13	18	3	1	1	1	4	1	1	----
Percent total area of remains	63	6	10	6	9	1	2	1	1	1	1	1	----

¹ <2 percent unidentified.
² cm².

sentative of the species composition of the surrounding vegetation.

In a closed canopy situation, only the very tops of the trees, those parts of the crowns visible from the air, are exposed to high-wind energies and hence have less leaves transported over long distances by wind. In open vegetation, all parts of the crown are exposed to wind energies sufficient 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 represent the actual area of the crown's surface exposed to the wind. If the shape of the crown approximates a sphere, then the projected crown area is roughly one quarter of the actual crown surface area. By the above argument, the litter source may be restricted to the upper hemisphere of the crown so that the projected area now approximates half the actual area. In closed canopies, this difference between the two areas becomes even less since only the topmost part of each crown is exposed and the crown shape is modified by the close proximity of other crowns. The leaf density varies throughout each crown, the distribution being dependent on species, habit, and proximity to adjacent trees.

It has been assumed that those leaves transported by wind originate from the outer surface of the crown. Whether this assumption is justified is open to question because no relevant data are available. What is clear is that on the basis of crown cover as defined, the error in estimating the size of the source for wind transport is likely to be greater for open vegetation than for woodlands that have closed canopy.

One way of correcting the estimate of crown areas to approximate more closely what the leaf litter production might be to weight 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 from known ground coverage. The dry weight, the form in which most litter studies are presented, may be similarly calculated. As pointed out, however, in nonriparian vegetation only litter produced in the upper parts of the crowns has a chance of being transported to the depositional site by wind.

RELATION BETWEEN PROJECTED CROWN AREAS AND LEAF DEPOSITION ON THE DELTA

By referring to percentage crown cover of trees with

distance from the delta, table 1, and numbers of leaves of these genera caught in traps, a direct comparison between the vegetation distribution and the leaves caught can be made. It is clear that the local species are grossly overrepresented. *Alnus* and *Salix*, with some *Quercus* and *Betula*, form the local species; of these, *Alnus* is the most abundant bordering the lake, hence its extremely high leaf count from the delta traps. *Salix*, by comparison, is underrepresented in the traps, undoubtedly because of the filtering action of the *Typha* bed. On the delta, *Salix cinerea* rarely attains a height greater than 4 m, and abundant *Salix* leaf litter was found among the *Typha* reeds. As expected, the more distant taxa, *Fagus*, *Aesculus*, and *Crataegus*, are underrepresented. *Quercus*, though more abundant some distance away from the delta, is a component of the local vegetation that, like *Betula*, occurs mostly behind the *Alnus* on the southeast lake shore. Once again, considerable filtering by lakeside vegetation reduces the probability that non-lakeside trees will be represented in the delta sediments.

When percentage crown cover (table 1) is compared with the summary statistics of leaves recovered from the delta sediments (table 3), a similar picture emerges. The species percentage, 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 overrepresentation of *Alnus* is still present. Species that are more distinct, but grow close to the stream, for example *Fagus* and *Quercus*, are now much less underrepresented than species of wider distribution, for example, *Betula*. The proportion of *Salix* whole leaves in the delta sediments is considerably higher than of those leaves arriving on the delta by wind transport alone (table 2); from this, it may be concluded that most of the *Salix* leaves represented in the delta were transported by the stream.

No clear quantitative relation exists between the number of leaves deposited on the delta and the vegetation as measured by the projected crown area. It is most unlikely, when one considers the large numbers of variables involved, that a simple direct relation between the deposited remains and the source vegetation can ever be found. The use of proportions to assess the relative representations of the taxa creates its own problems, because, being a closed system, a departure from a direct relation exhibited by one species necessarily affects the others. Failure to derive relations 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 common a plant was in the past, it may yet be possible to determine

where it grew relative to the depositional site and thereby discover paleocommunity relations.

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, for example, that the grains approximate spheres and do not interfere with each other. And 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.

Mantz (1973) has shown that for solid shapes that depart only slightly from a spherical form (but which may still be described as having a single geometric length dimension), the shape effect on entrainment is minimal. For shapes that 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. Schoklitsch and Shields 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, oral commun., 1975). Mantz (1973, 1977) 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. If leaves behave similarly, then considerable sorting would result, solely on the basis of shape, between, for example, leaves and fruits. It should be noted, however, that all workers have used plane sedimentary beds (defined as plane to within one solid particle diameter), a condition that rarely, if ever, exists in nature.

The effect of leaf orientation and aspect on fluid flow clearly determines the critical fluid stress at which the leaf will begin to move. Elongate 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. Since the object presents a smaller area to the fluid flow, the fluid stresses on the object are low and movement begins at correspondingly greater fluid velocity.

Many fluid-dynamics equations require that an effective geometric dimension be ascribed to the sedimentary particle under investigation. For a sphere, this dimension is the diameter. It is difficult to directly ascribe such a length dimension to an essentially two-dimensional object such as a leaf, because the effective value of this parameter will vary with the orientation of the object to the fluid flow. The fluid flow (fig. 14) will affect the orientation of the object because the turbulent wake will impart instability to an un-fixed plate (such as a leaf), with the result that its orientation with respect to the fluid flow will continually change. Such a condition may be observed in leaves falling in still air. If the terminal velocity of a

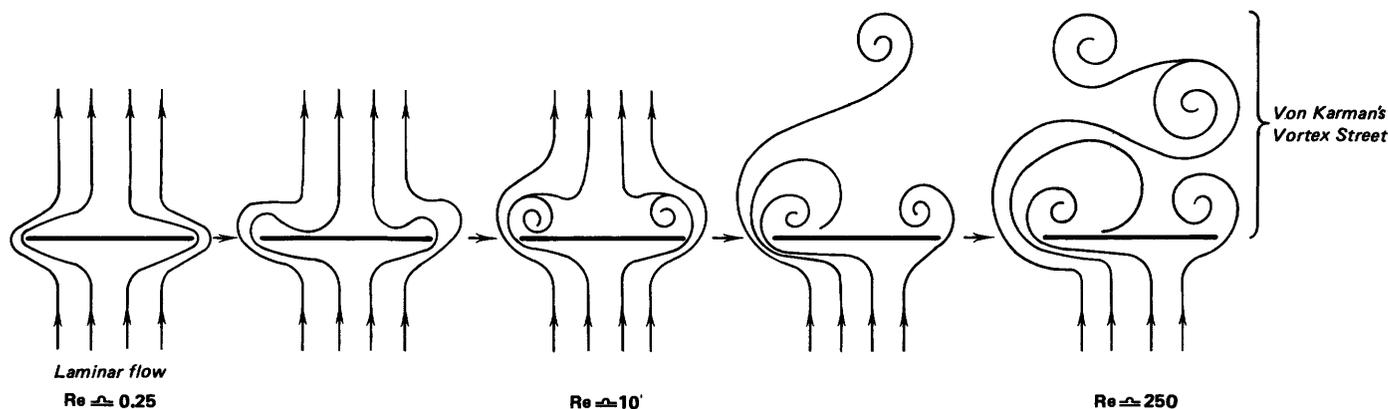


FIGURE 14.—Stream lines around rigid plate held normal to fluid flow. As Reynolds number is increased, here achieved by increasing flow past plate, eddies form in lee of plate. At first these eddies are small and symmetrical, but as fluid flow is further increased, they become unstable so that at high Reynolds numbers, a series of unequal eddies stretch along wake behind plate. After Batchelor, 1967, plate 4. The Reynolds number is a dimensionless number that may be interpreted as being proportional to the ratio between inertial and viscous forces given by

$$Re = UL\rho/\mu$$

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

leaf is such that a turbulent wake is produced, then the leaf will flutter or spin to the ground, whatever the attitude at which it begins to fall or turbulence in the surrounding air.

Mantz (oral commun., 1975) 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. Mantz used this to examine the entrainment of dry autumn leaves by wind:

"An estimate was made of the critical wind stress (τ_c) which produces initial transport of surface leaves from a bed of natural autumn leaves. An anemometer placed at 40 cm above the leaf bed surface was used to record the wind velocity on 20 occasions when surface leaves were first transported. The Karman-Prandtl velocity distribution law was then used to estimate the associated average wind stress as 0.3 N/m^2 . The average leaf statistics were 0.13 m length, 0.00017 m thickness, and 450 kg/m^3 density (σ). These were used to estimate the Shields (1936) critical stress parameter ($\theta_c = \tau_c / \sigma g D_n$, where D_n is the nominal diameter for a leaf) as 0.004. Such a value is an order of magnitude below that for the incipient transport of natural flakey minerals under water (Mantz, 1977). The result is however to be expected for the main reason that a natural leaf bed packs more loosely than a natural mineral bed." (P. Mantz, Imperial College, written commun., 1980).

Berthois (1962) found little similarity in hydraulic behavior of approximately spherical quartz particles and mica grains of the same nominal diameter. Experiments on mineral solids that do approximate spheres indicate that transport behavior often cannot be predicted better than to within one order of magnitude; thus similar predictions for leaf transport may be greatly in error.

The settling of leaves in water is further complicated by the fact that as leaves become saturated, the density of the leaf will alter not only with time but also from place to place within the leaf. The deposition of sediment particles on the surface of the leaf and invasion of the tissues by microorganisms will also affect the density. These factors, together with the natural variation in size and shape and the flexible nature of leaves, make assigning a characteristic length impossible; even under ideal conditions, where fluid turbulence is minimal, the behavior of leaves cannot be described by simple equations of fluid dynamics.

Despite 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 that may prove useful in determining the relative source areas of the component species.

The concept of hydraulic equivalence may be employed to determine the predominant transport medium of various plant species in relation to the en-

tombing 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. 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, 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. On the lake bottom, where the fluid stresses are small, the sunken leaves are likely to exhibit a wide range of hydraulic characteristics.

If a population of fossil-leaf remains is judged to have the same hydraulic equivalence as the sediment grains composing the surrounding matrix, then it is probable that both were deposited in response to the same fluid medium. Under certain circumstances, it may be possible to determine the transport medium (air or water) for a particular group of remains and thereby gain a clue as to the species distribution within the source of vegetation.

It is unlikely that the hydraulic characteristics of plant remains can be theoretically deduced; consequently, an empirical approach to the investigation of sorting is required.

WIND TRANSPORT

The role of wind transport in the dispersal of fruits and seeds has long been recognized (Ridley, 1930); 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 megascopic plant remains, the dispersal of leaves as such has attracted little attention.

Although it cannot be expected that leaves will be transported long distances by wind, populations of leaves from different species may be carried significantly different distances, and a distorted picture of the source vegetation may be presented by an allochthonous assemblage. The preliminary investigations into the possible causes of differential leaf dispersal described here were carried out in conjunction with Dr. D.K. Ferguson at the Rijksuniversitair Centrum Antwerpen.

Wind transport can 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

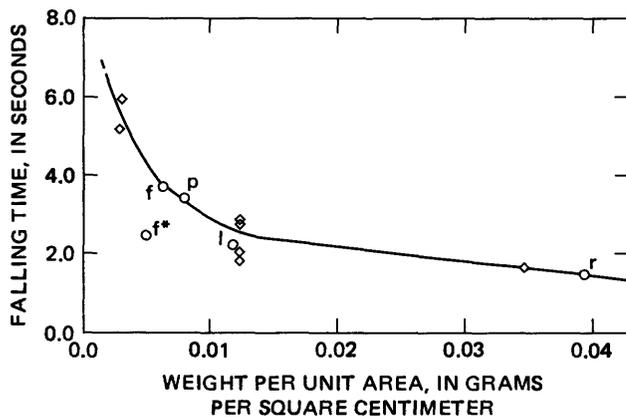
carried out using artificial leaves, the parameters of which could be controlled within narrow limits. "Leaves" made of air-mail paper (0.0030 g/cm²), cartridge paper (0.0123 g/cm²), and card (0.0346 g/cm²) were used, cut into circles, equilateral triangles, and two rhombic shapes of length to breadth ratios of 1.45:1 and 6.90:1. In most experiments, two sizes of each shape were used, 11 cm² and 44 cm²; some additional measurement were made using units of 22 cm². The time taken for the units (which were released with their flat surfaces horizontal) to fall an arbitrary vertical distance of 3.18 m in still air was recorded and the results plotted as figure 15.

Once on the ground leaves may be blown laterally. An attempt to investigate this aspect of dispersal was made by blowing leaves, both artificial and natural, along a plane flat surface using a ducted fan, moved from side to side over a distance of 3 m for a period of 1 minute so that all the units were blown evenly. Although the air flow from this fan was extremely turbulent, and by no means uniform, the relative dispersal of the units could be determined; the results are shown in figures 16 and 17.

The results 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



EXPLANATION

- ◇ Paper leaves
- Natural leaves
- r *Rhododendron*
- l *Laurus nobilis* L.
- p *Platanus X hispanica* Muench
- f *Fagus sylvatica* L. (flat)
- f* *F. sylvatica* (curled)

FIGURE 15.—Time taken for leaves (both paper and natural) to fall a distance of 3.18 m in still air plotted relative to their weight per unit area.

in the air as well as to broaden the ground dispersion. These differences are insignificant, however, when compared with those resulting from variations in weight.

Flat shapes blown horizontally along the ground were distributed laterally by a combination of saltation and rolling; the greatest lateral dispersion was found with circular shapes that tended to roll. When the flat shapes were folded such that when viewed along the axis of the fold a V shape was formed, the distance they were transported increased for a given windspeed but imbrication caused a marked positive skewness in the histogram (fig. 17). A similar effect was noticed for *Fagus* leaves that had curled during drying.

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 tendency to be more stable in the air and generally remained horizontal while fall-

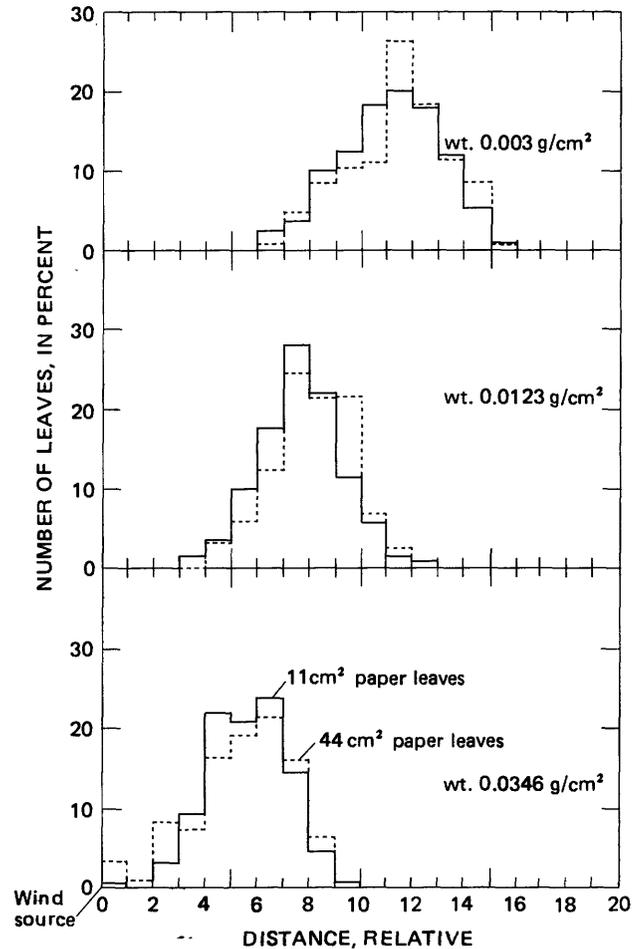


FIGURE 16.—Lateral blowing of flat rhombic paper leaves (length-to-breadth ratio 1.45:1) along a plane flat surface. Horizontal distance leaves will travel will be dependent on wind strength; distance classes arbitrary.

ing after being released in that position. This behavior was observed 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 determined by differences in weight per unit area more

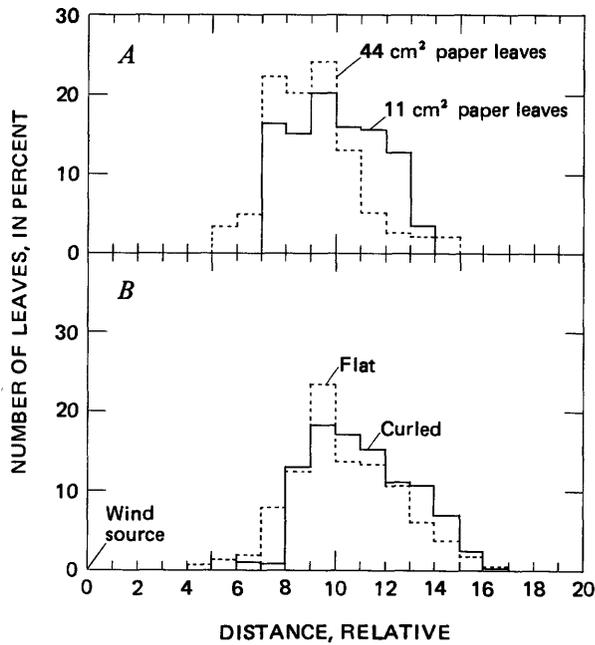


FIGURE 17.—Horizontal distance traveled by folded paper (0.0123 g/cm²) as compared with both flat and curled *Fagus* leaves under influence of a given wind speed. A, Folded paper; B, *Fagus* leaves. Curled *Fagus* leaves appeared to be blown fractionally farther than flat leaves, but imbrication caused marked positive skewness.

than any other single factor. Shapes made from card, the heaviest material, showed little variation between sizes, shapes of air-mail paper more, possibly because of relative increase in importance of size at low-weight levels. As would be expected, shapes with a greater weight per unit area fell faster, while the lightest shapes took correspondingly longer. The relation does not appear to be linear (fig. 15).

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 traveled. Increasing weight caused a progressive shift in the mean of the distributions toward the wind source (fig. 16), which, because the wind energy in this experiment was inversely proportional to the distance from the source, means that the wind velocity that is necessary to bring about incipient movement is proportional to the weight per unit area of the dispersal unit.

All artificial paper leaves used in the above experiments 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

Considerable differences may exist in leaf weight per unit area and size between sun and shade leaves within a single species, for example, *Fagus sylvatica*. The leaves at the top of the crown of many trees tend to be smaller and have a greater weight per unit area than those lower down, particularly in a dense forest

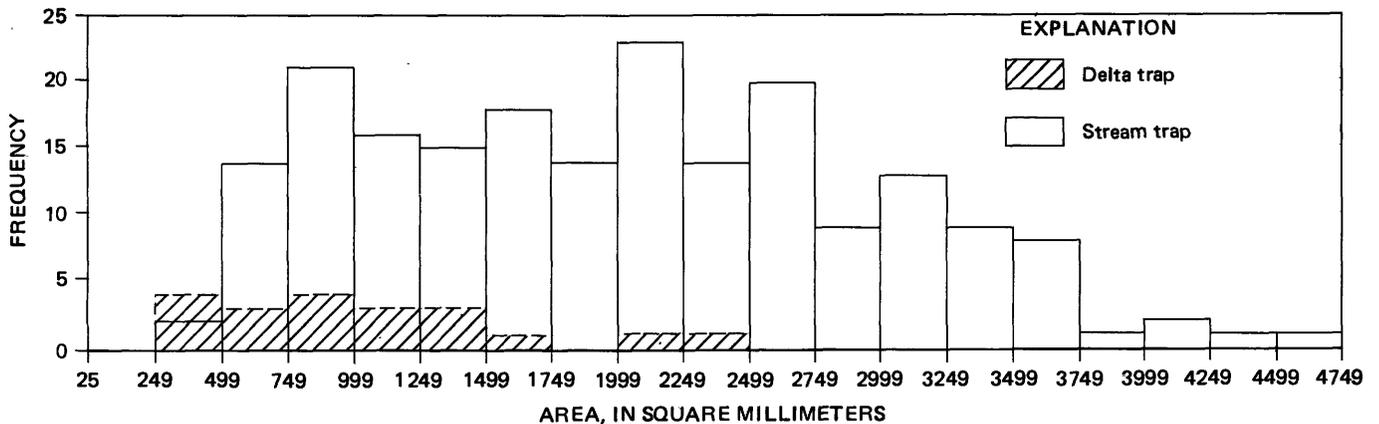


FIGURE 18.—Size-frequency histogram for *Fagus sylvatica* leaves recovered from both stream and delta traps. Stream trap was positioned in a part of stream that flowed past a stand of mature trees forming a closed canopy over stream; sample may be considered to be representative of litter on woodland floor. Following 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 because the observed statistic d (= 6.94) exceeded the published value at the 1-percent level of significance.

canopy. Despite these differences, the top leaves have a greater chance of wide dispersal because they are exposed to higher wind energies than those within the canopy or trunk space. Most leaves of distant species, such as *Fagus sylvatica*, caught in the delta surface traps were small sun leaves, not, as might be expected from the laboratory experiments, leaves of a smaller weight per unit area (fig. 18).

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-percent probability level (fig. 18). It cannot be argued that the leaves in the delta traps represented a sample from a group of *Fagus* trees that might bear only small leaves, because the absence of any strong prevailing wind direction during the sampling period suggests that the sample was representative of the surrounding vegetation (fig. 19 and table 4). *Alnus* leaves from the delta traps are compared in figure 20 with a sample 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 enters the lake than is representative of the litter from the surrounding vegetation, although the difference may not be significant.

The representation of at least part of the flora by only the small dense leaves has critical consequences for paleoclimatic interpretations based on fossil deposits. Dilcher (1973) discusses the correlation of leaf size with climate and demonstrates how both temperature and moisture influence the relation. The wet tropics are characterized by a high percentage of large leaves, whereas a change to a drier or cooler climate is accompanied by an increase in percentage of small leaves. Wolfe (1971) recognized the problems 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 streamside plants (MacGinitie, 1953, p. 46) [such as] stenophyllous plants that typically fall into the low size-classes (Richards, 1966)***. Such over-representation would yield an analysis indicating a cooler climate***."

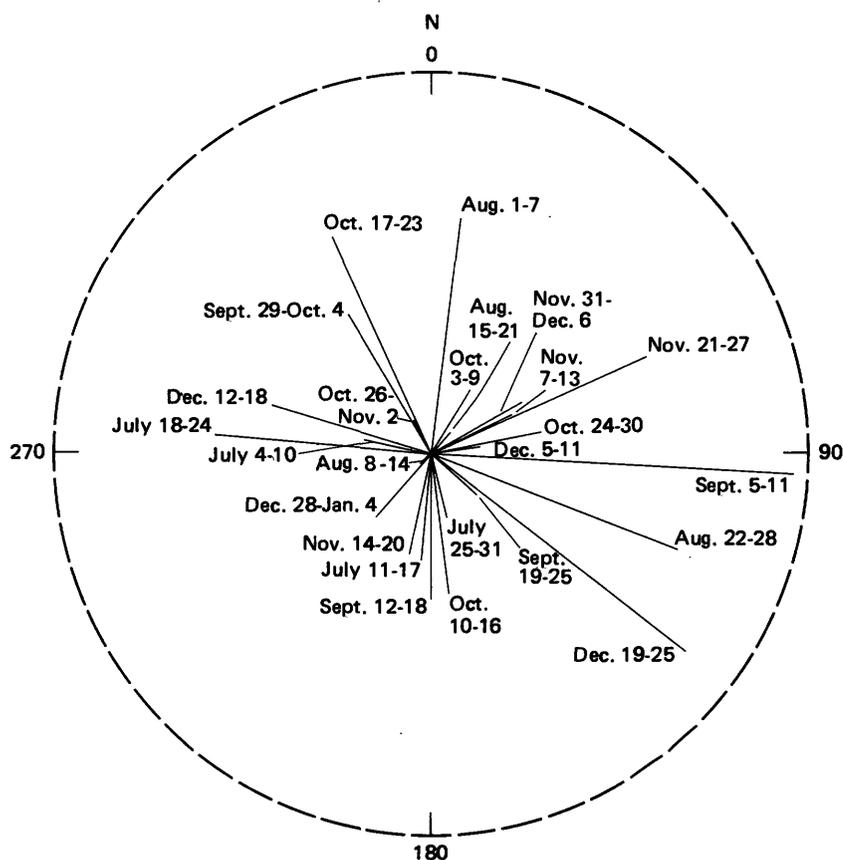


FIGURE 19.—Mean weekly wind directions for July to December 1973 as computed from data collected at Heathrow Airport, London. Actual values, together with mean angles of deviation, presented in table 4.

TABLE 4.—Mean weekly wind directions for July to December 1973 as measured at Heathrow Airport, London

(*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 center of a unit circle (with a radius of 1))

	(1973)	Mean direction (degrees)	<i>R</i> (fig. 18)	Mean angle of deviation (degrees)
July	4-10	282	0.10	76.9
	11-17	184	.14	75.0
	18-24	275	.29	68.0
	25-31	165	.09	77.2
Aug	1-7	7	.32	66.5
	8-14	221	.03	79.6
	15-21	31	.05	78.8
Sept	22-28	110	.36	64.6
	29-4	329	.22	71.5
	5-11	93	.49	57.8
Oct	12-18	179	.20	72.4
	19-25	129	.07	77.9
	26-2	333	.05	78.9
	3-9	30	.10	76.8
Nov	10-16	172	.19	72.7
	17-23	335	.31	67.1
	24-30	78	.15	74.4
	31-6	64	.12	75.7
Dec	7-13	60	.14	74.8
	14-20	192	.14	74.8
	21-27	66	.32	66.8
	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	0.03	79.4

Dilcher (1973) points out that in the clay deposits of Kentucky and Tennessee leaves of greatly different size classes occur 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. 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 fluvial environment in which the larger leaves would tend to be destroyed. In any case, it is impossible to prove, from a fossil flora, that overrepresentation has, or 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 nearly representative of the forest litter. In more open waters, distant components of the surrounding flora are represented only by the smaller leaves, as a result of differential aerial transport. While it is difficult, in the absence of any positive evidence, to endorse Wolfe's assumption that overrepresentation of small leaves results from overrepresentation of streamside plants, differential aerial transport of leaves from the more distant species

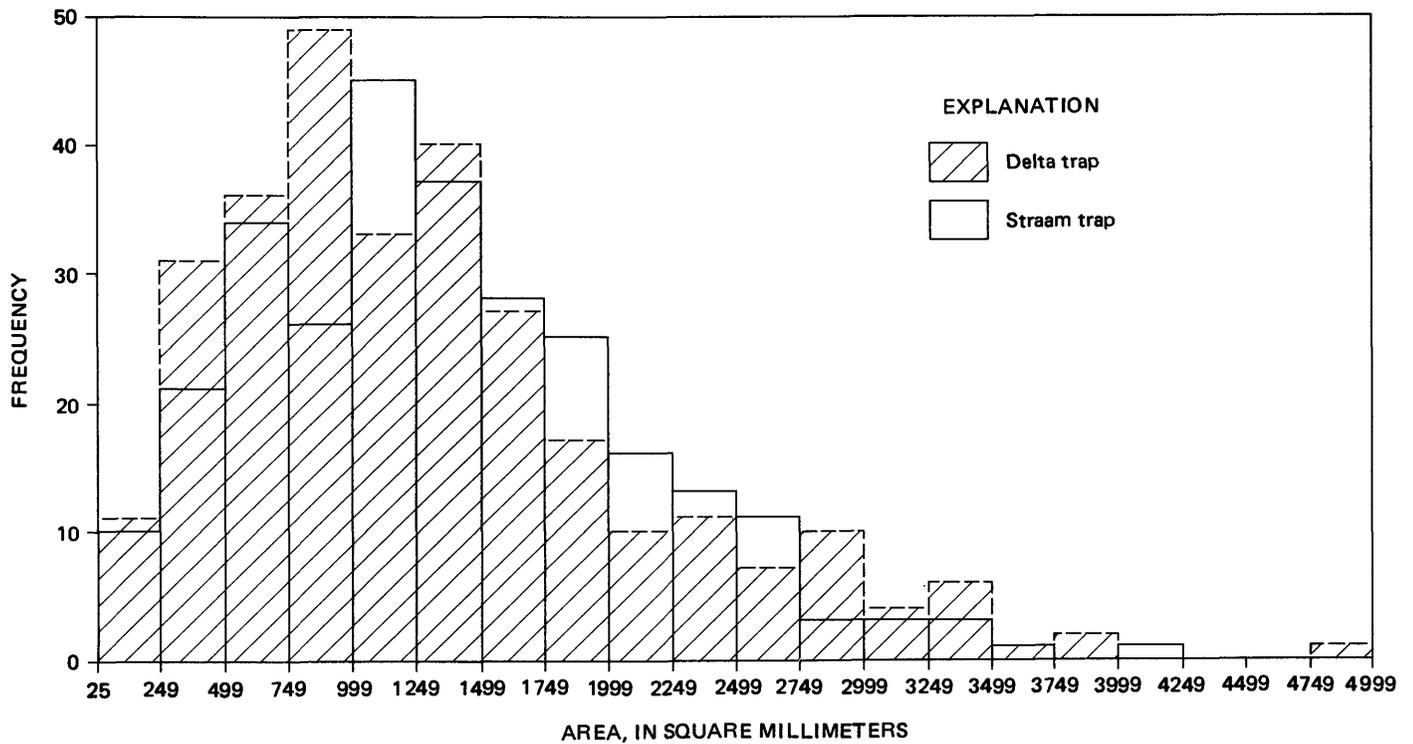


FIGURE 20.—Size-frequency histogram for *Alnus glutinosa* leaves recovered from both stream and delta traps. Distributions are similar with perhaps a slight positive skewness exhibited by delta sample. Fisher-Behrens test showed no significant difference in the means ($d = 0.56$).

can bring about a similar effect, with the result that the fossil flora may be interpreted as apparently representing a cooler or dryer climate than actually existed.

Trees growing around a lake margin can contribute leaves to the lake sediments by direct leaf fall and minimal lateral transport. The leaf population derived from such trees will closely resemble that found on the forest floor and, as such, will consist of both "sun" and "shade" leaves. Lacustrine sediments deposited in small basins are consequently likely to contain a population of fossil leaves that reflects the full size range of leaves, at abscission, in the original forest. Swamp deposits will similarly contain a minimally biased sample of the leaves from the source plants. Conversely, deposits laid down in basins where the minimum lake width is large relative to the canopy height will be relatively enriched with sun leaves from both the locally and distantly growing source taxa.

If the local community is restricted in area or leaf productivity, then its contribution to the fossil assemblage may dilute out, an effect analogous to that described by Neves (1958), Chaloner (1958), and Chaloner and Muir (1968) for spores.

Climate will affect the dispersal of leaves because conditions of high humidity will increase the weight per unit area of the leaves. If liquid water is present, their ability to be transported by aerial saltation and rolling will be seriously diminished because they will tend to cling together and to any substrate as a result of 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 that 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 D. K. Ferguson (unpub. data 1973) has shown that leaves of *Laurus nobilis* L. will be trapped only on the windward side of a diffuse obstacle, such as a bush, provided that the windspeed is low (10 km/hr). Speeds exceeding this rate create a buildup 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 because wind energy is dissipated in turbulence behind the obstacle leading to a deposition of the "suspended" load. Pollen, being so much smaller, has a much slower settling velocity and is likely to pass through mostly unaffected.

Some workers have used a negative exponential decay model to describe the decrease in deposition of windborne plant material as a function of distance from the source (Richerson and others, 1970; Edmonds and Benninghoff, 1973; Rau, 1976). The form of the equation used by Rau (1976), who studied litter deposition in a lake, is

$$Z_x = Z_r \exp(-k[r-x])$$

where x = distance from the lake center, Z_x = deposition occurring at distance x , r = distance from the lake center to the shoreline, Z_r = deposition at the shoreline, and $k = -(r-x)^{-1} \ln(Z_x/Z_r)$.

The curve of figure 21 shows the relationship between the observed windborne leaf deposition on the delta at Silwood and the expected deposition as predicted by a least-squares best fit of the negative exponential model. Although the fit was fair ($r^2 = 0.91$), variations in the observed data could well have been produced by the close proximity of the hydrosere vegetation on the delta.

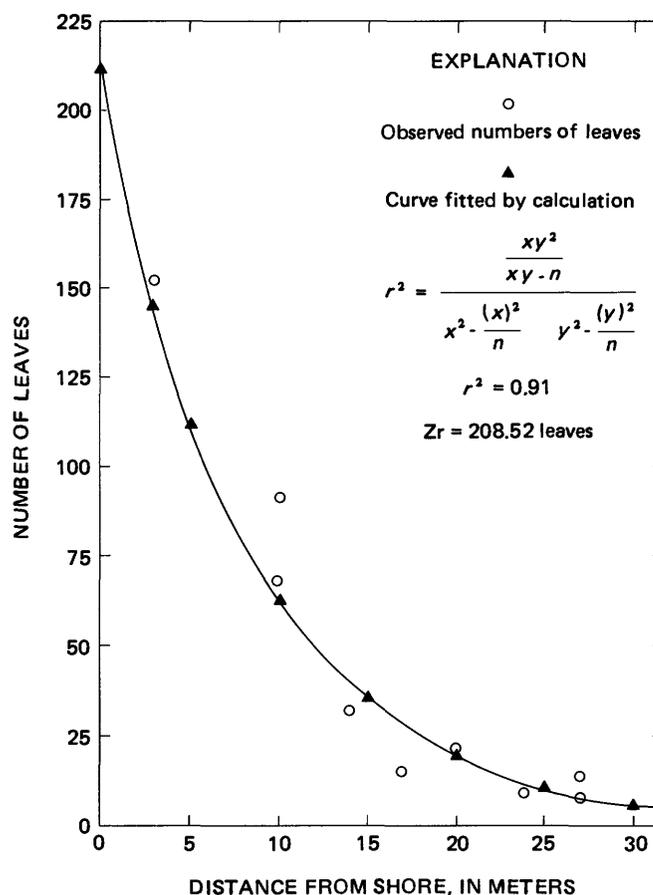


FIGURE 21.—Deposition of leaves onto delta surface by wind as a function of distance from north shore of Silwood Lake. Observed leaf deposition compared with that predicted by a negative exponential model (Rau, 1976). Coefficient of determination, r^2 , is an estimate of how closely equation fits experimental data and varies between 0 and 1. The closer r^2 is to 1, the better the fit.

This model describes only the pattern of leaf deposition onto a water or land surface and does not necessarily relate to the distribution of plant material on the lake bottom. Subsequent redistribution of floating leaves by wind or water currents and degradation on the lake bottom may invalidate the application of the negative exponential model to the description of the distribution of organic matter on the lake bed; further redistribution of the more finely divided plant material may be brought about by water currents set up during thermal overturn.

EFFECT OF THE DECIDUOUS HABIT

None of the leaves examined from the Silwood deposits could be assigned with certainty to any herbaceous species. The importance of leaf-shedding habits of plants in affecting their chances of representation in the fossil record has been noted by other workers (for example, Chaney, 1924, and Ferguson, 1971). The lack of deciduous habit results in leaves of herbaceous plants withering and disintegrating while still attached to the stem; hence, the extreme rarity of herbaceous plants in sedimentary environments. Many deciduous trees also fail to shed leaves, particularly when juvenile (for example, *Fagus sylvatica* and *Quercus robur*), which must in turn distort the fossil record.

The evergreen species do of course shed their leaves, usually not in the autumn but when new growth begins. *Ilex aquifolium* L., for example, commonly sheds its leaves in the spring. 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, 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 while the remainder shed their leaves during the dryer part of the year. The spring fall of *Ilex* may well lead to a different dispersal pattern than exhibited by leaves shed in the autumn months.

WATER TRANSPORT

Botanists have long recognized the role of water in the transport and dispersal of plant material. Berry (1906) observed large "rafts" of leaves being transported downstream by river waters, and 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, p. 4-8).

DISCUSSION OF LEAF-FLOATING EXPERIMENTS

Moseley (1892), while on board H.M.S. *Challenger*, observed the transport of plant debris offshore 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 is therefore well established.

Preliminary experiments with *Fagus sylvatica* leaves have shown 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 rare in nature, being found only 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 gas-saturated water, significant increases in floating time may result from the formation of gas bubbles on the leaf. Using the light-beam apparatus (fig. 6), it was found that this phenomenon caused previously sunken leaves to re-float. In order to achieve consistent results and thereby make valid the comparisons of floating times between species, it was necessary to agitate the water surface periodically. Unfortunately, even minimal agitation caused flow currents to be set up in the water 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 of only limited use. The effect of turbulence and air bubble formation is demonstrated in figures 22, 23, and 24.

In the turbulent surface waters of a lake or river, 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 most laboratory bucket experiments. From the results of such experiments and the range of floating times as shown in figures 22, 23, 25, and 26, the sinking pattern commonly resembles the cumulative log-normal distribution curves typical of dosage response.

At first it was considered suitable to analyze such curves using probit analysis. However, the design of the experiments was such that this was inappropriate

(Finney, 1971, p. 27). If the experiments were redesigned to conform to the form required for probit analysis, that is, 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, in this case the length of time taken for 50 percent of the leaf population to sink, 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 different 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 means, however, that little precision in paleocommunity reconstruction is likely to be achieved by studying this aspect of dispersal. Analyses of floating times are critical 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. It should be born in mind, however, that

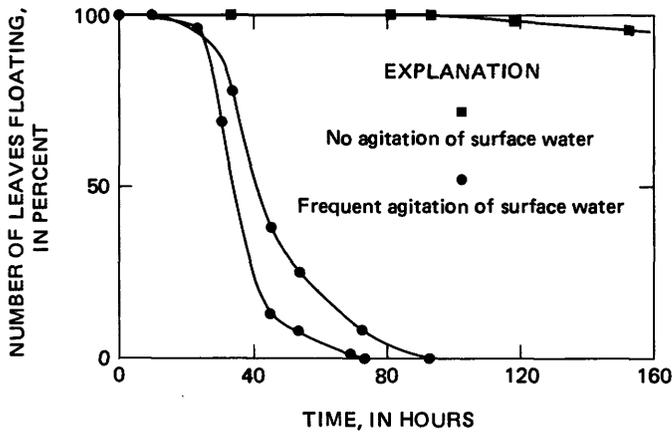


FIGURE 22.—Effect of water turbulence on floating time of air-dried *Fagus sylvatica* leaves as determined from bucket experiments.

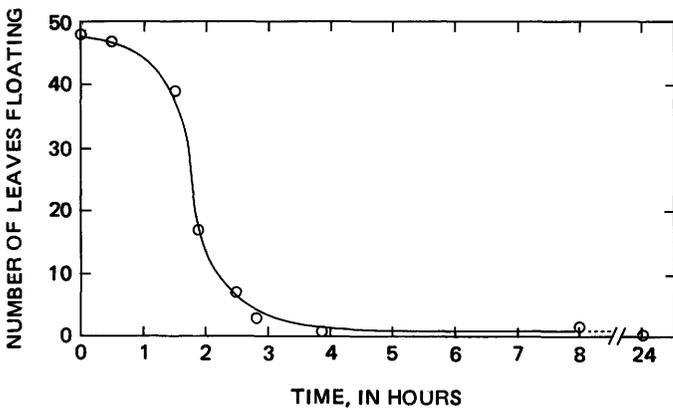


FIGURE 23.—Floating time of *Alnus glutinosa* leaves in experiment carried out in a bucket with frequent agitation.

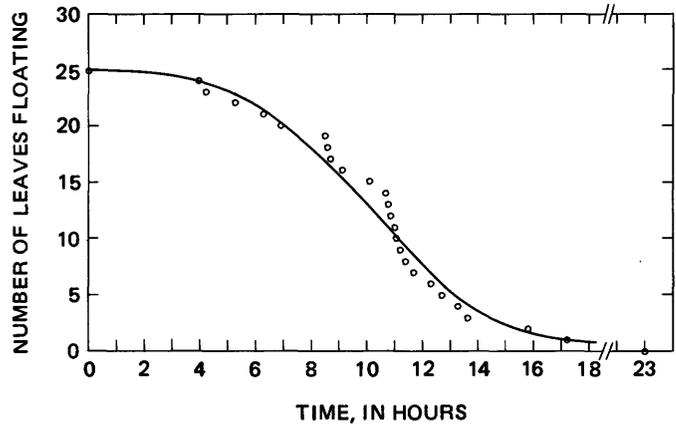


FIGURE 24.—Floating time of *Alnus glutinosa* leaves in experiment carried out in light-plane apparatus with no agitation. Line fitted by eye.

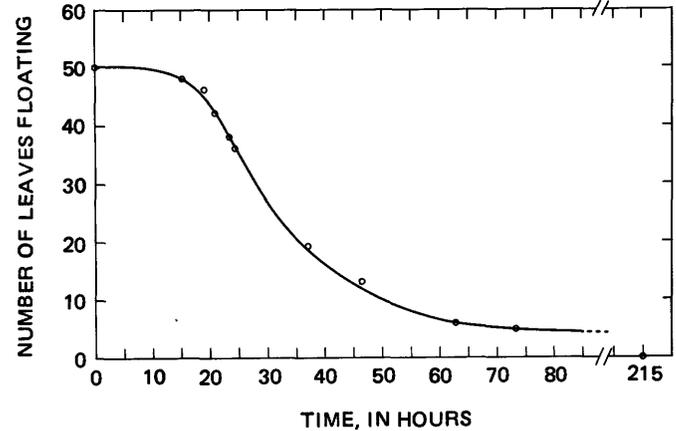


FIGURE 25.—Floating time of freshly fallen *Ilex aquifolium* leaves in experiments carried out by bucket method with frequent agitation. Line fitted by eye.

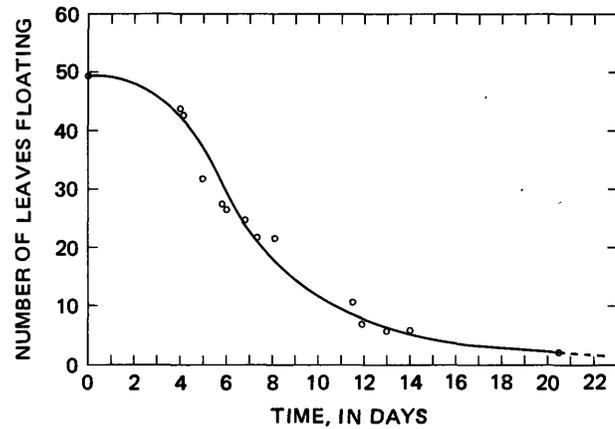


FIGURE 26.—Floating time of freshly fallen *Rhododendron* sp. leaves as recorded from a bucket experiment with frequent agitation.

perhaps the greater part of water transport occurs during that period of time when the leaf is either in suspension or is part of the bedload. Casual observation showed that at any given time, even during the autumn, far more leaves were present in the Silwood stream as part of the bedload than were floating.

LEAF DEGRADATION, BIOLOGICAL, CHEMICAL, MECHANICAL

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 paleobotanical problems. Weight losses may occur owing to leaching of soluble substances, for instance, which may not directly affect the chances of 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 escaping destruction will clearly determine whether or not the species is recognizable in the fossil record.

Petersen and Cummins (1974) have studied leaf degradation by constructing 10-g artificial leaf packs of single species (held together with a nylon fastener) and measuring 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 (for example, Mathews and Kawalczewski, 1969). This approach has the advantage that access by degrading organisms can 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 degradation may not proceed as it would 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. Nearly rigid nylon cages (0.5-cm² mesh size) were used to allow all but the largest invertebrate detritivores access, at the same time retaining all the identifiable leaf fragments. The semirigidity of the cages insured that the leaves were, to some extent, protected from mechanical breakdown (except that caused by abrasion between themselves). This protection was desirable because estimates of the mechanical strength of the leaves were to be deter-

mined 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 measured only breakdown in terms of the visible leaf-lamina loss, not internal tissue destruction as might be caused by microorganisms. 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.

Biological

The dominant food energy source of a small woodland stream is the allochthonous input (see Egglisshaw, 1964; Cummins and others, 1972, 1973), and it has been demonstrated that the aquatic insect community becomes synchronized to the autumnal input of leaf material (Hynes, 1961), emergence, oviposition, and eclosion occurring just prior to leaf abscission. The type of leaf degradation caused by invertebrate organisms may be classified as that brought about by the activities of large particle feeders and that produced by small particle feeders (Yonge, 1928; Petersen and Cummins, 1974). The activity of both these groups of organisms may be seen in figures 27-36. The large rounded holes are typical of the large particle feeders, while the removal of predominantly intercostal tissue only is the result of the activities of the small particle feeders. Sometimes attack appears to begin at the margins (for example, fig. 32, lake 1 month), but extensive damage to the lamina rapidly takes place; by the fourth month in the lake environment, some leaves are extensively degraded. 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 (for example, fig. 31, stream 4 months).

It can be seen that the degree of degradation that takes place over a given time 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. Kaushik and Hynes (1971) demonstrated that stream invertebrates such as *Gammarus* exhibit a preference for certain species that reflects the susceptibility of those species to colonization by fungi, which are more damaging than bacteria during the initial stages of breakdown. Barlocher and Kendrick (1974) have confirmed these findings, show-

ing that those areas of leaves with a high hyphal content are preferentially consumed by invertebrates. If leaves are fragmented, the initial rate of decay is increased, but this effect does not extend beyond a few weeks (Kaushik and Hynes, 1971).

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 as well as the chemical nature of the material, especially the nitrogen content (Waksman and Tenny, 1927; Waksman

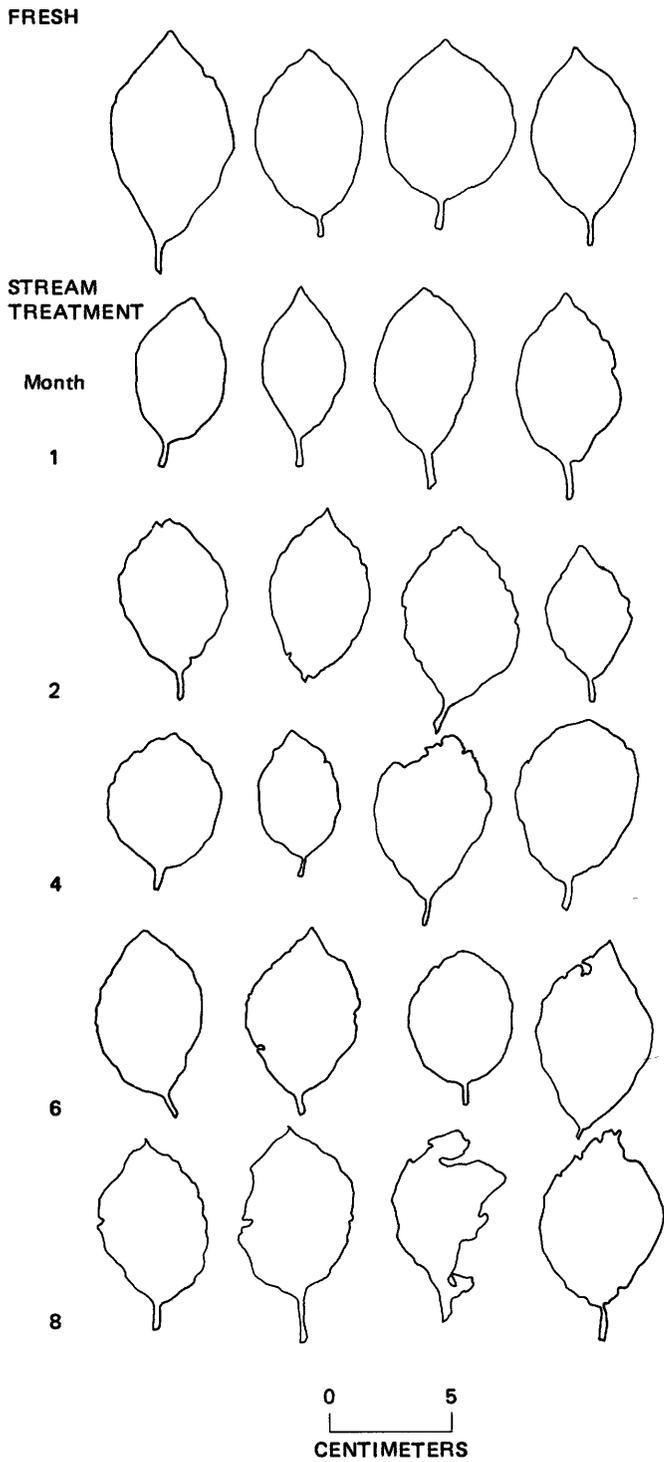


FIGURE 27.—Outline of *Fagus sylvatica* leaves showing area of lamina loss after various periods of exposure to stream environment.

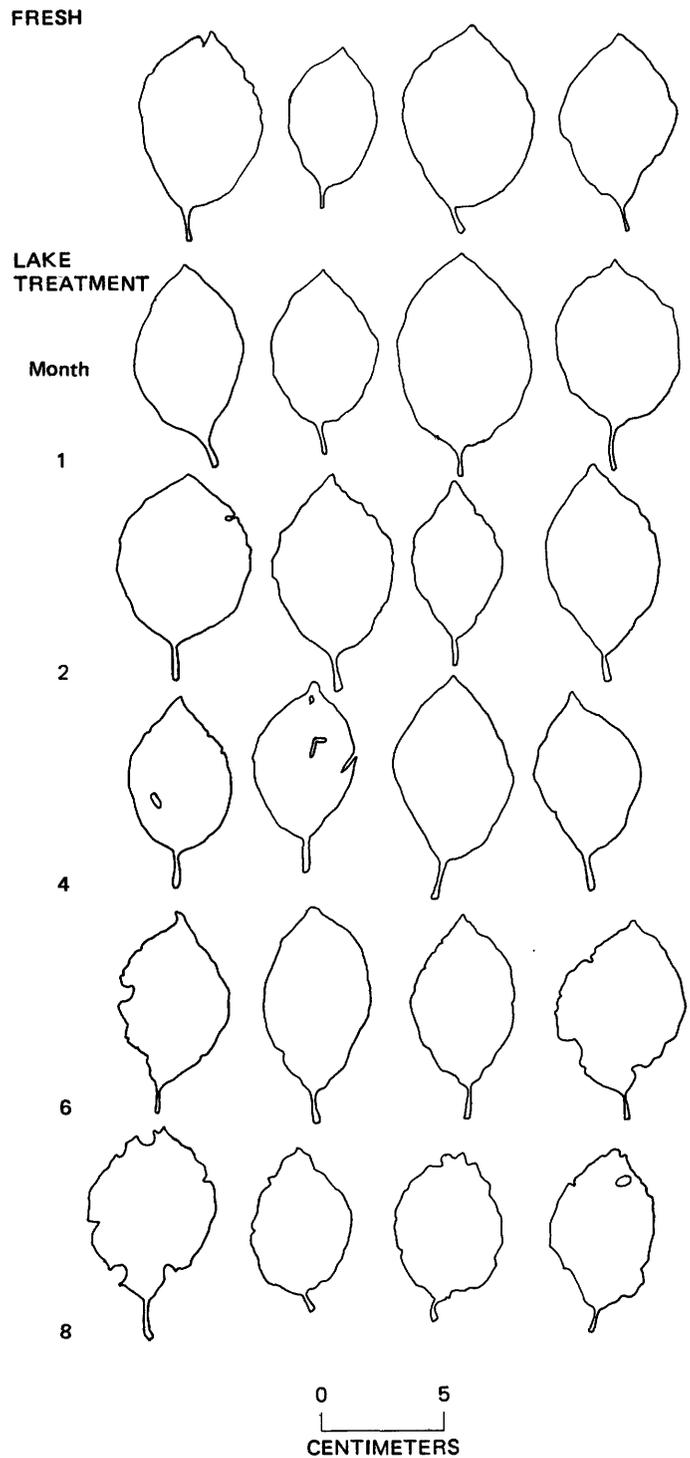


FIGURE 28.—Outline of *Fagus sylvatica* leaves showing area of lamina loss from exposure to lake environment.

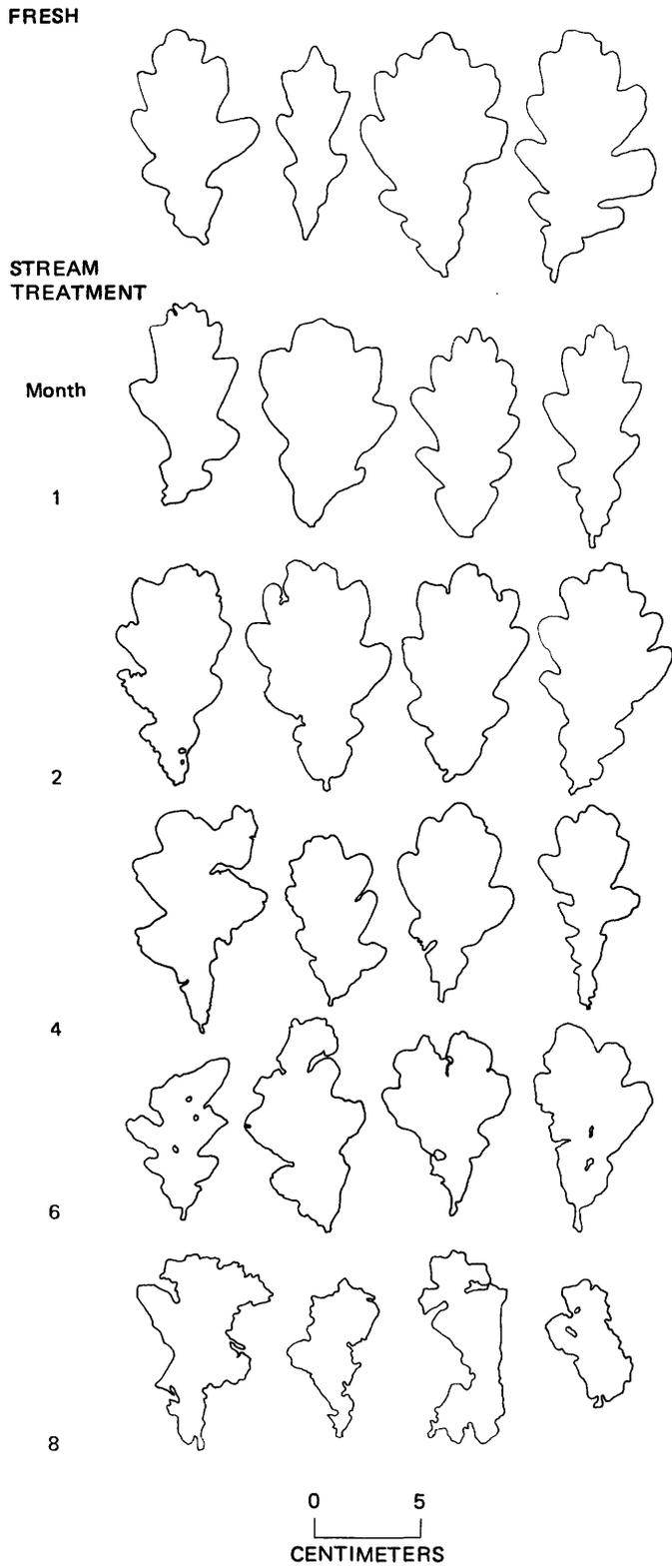


FIGURE 29.—Outline of *Quercus robur* leaves showing area of lamina loss after various periods of exposure to stream environment.

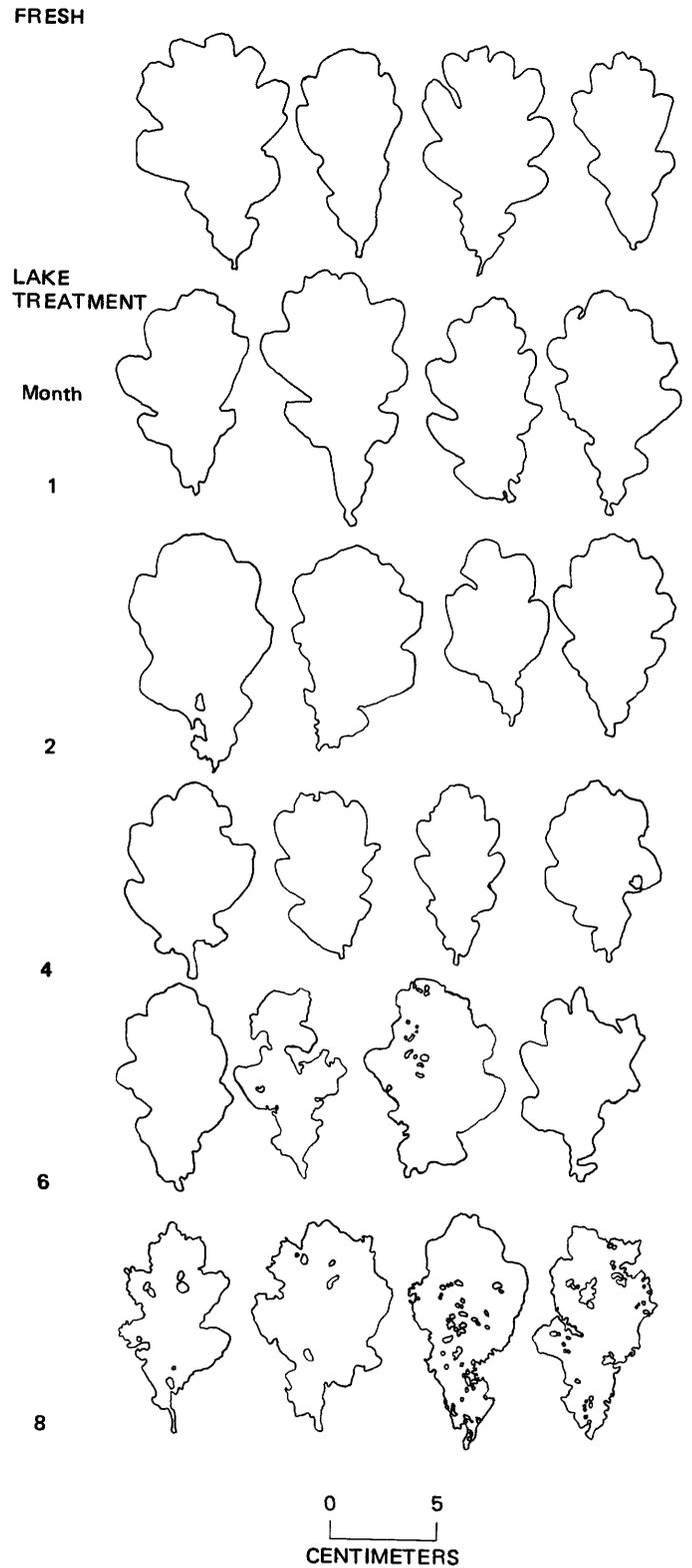
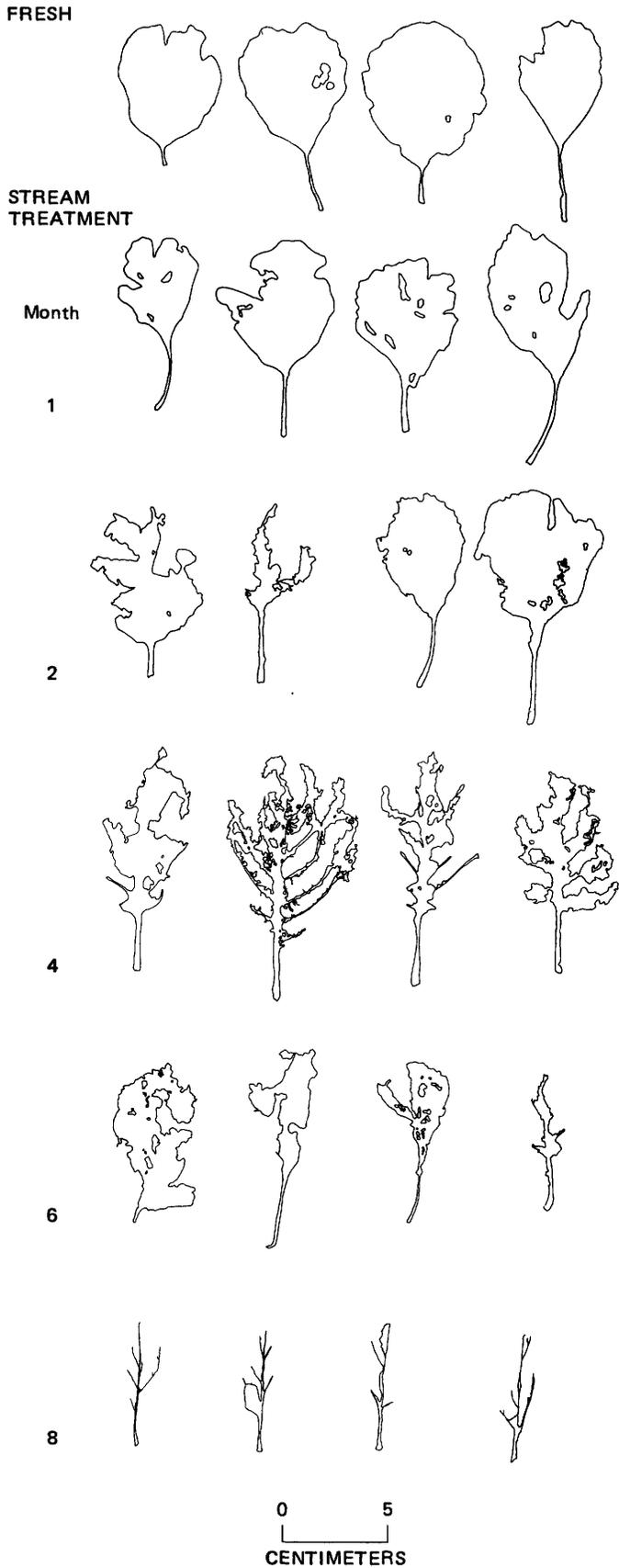


FIGURE 30.—Outline of *Quercus robur* leaves showing lamina loss after various periods of exposure to lake environment.



and others, 1928; Melin, 1930). Melin (1930) found that within a species there was a direct relation between the amount of nitrogen in the material and its rate of breakdown, but between species this relation was not so clear, as other factors, such as the amount of lignin

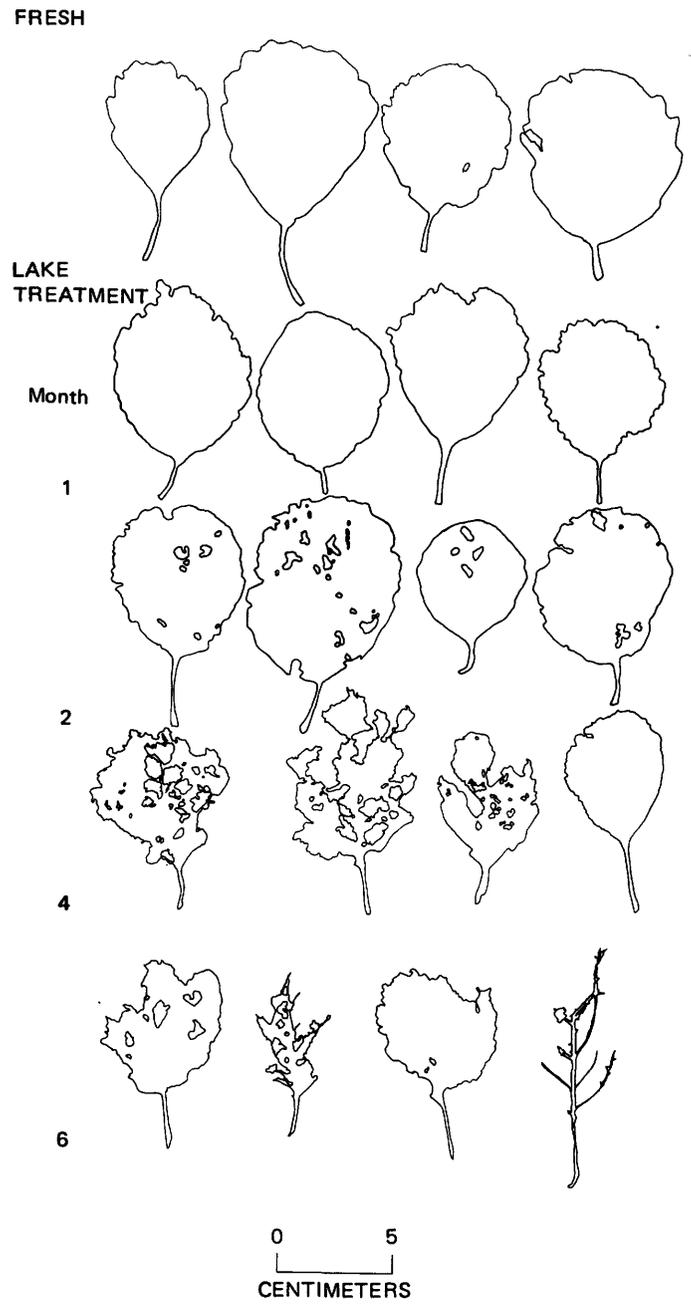


FIGURE 32.—Outlines of *Alnus glutinosa* leaves showing extent of degradation after various periods of exposure to lake environment conditions. After 8 months, only fragments were left.

FIGURE 31.—Outline of *Alnus glutinosa* leaves showing extent of degradation after exposure to stream environment for various lengths of time.

or antifungal compounds present, affected microbial colonization. Mathews and Kawalczewski (1969), using bags with different mesh sizes, found that although bags with a coarse mesh size (3 mm) gave access to a greater invertebrate fauna, the leaves did not break down any more rapidly than in bags with a fine mesh size (0.27 mm). They concluded that most losses (dry weight) are caused by microbial activity. They also noted significant increases in the nitrogen content of the leaves, presumably by uptake of nitrogen by increasingly large numbers of microorganisms. If nitrogen is added to a system in which leaves are decaying, the rate of breakdown is increased to a maximum rate that is in part species dependent. This effect is further enhanced when phosphorus is added to the system (Kaushik and Hynes, 1971).

FRESH

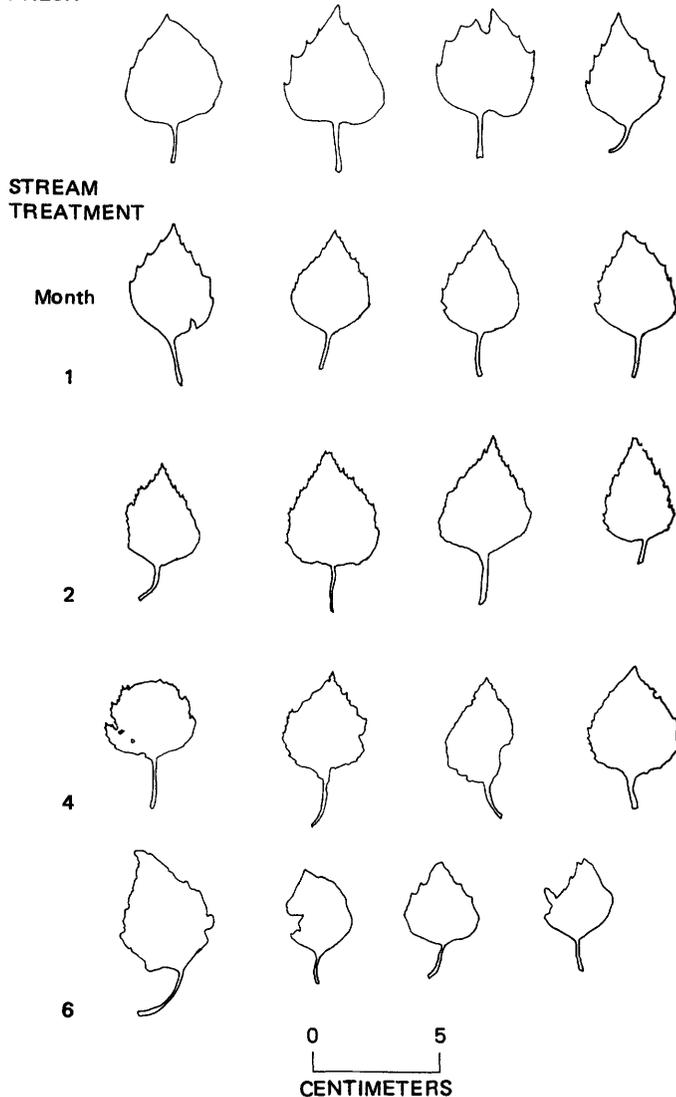


FIGURE 33.—Outline of *Betula pubescens* leaves showing progressive lamina loss in stream environment. After 8 months, only fragments were left.

Chemical

The rate of invertebrate leaf degradation is controlled by microbial conditioning, and the rate of microbial colonization seems to be dependent on the chemical composition of the leaf. As Nykvist (1962) has shown, however, the chemical composition of leaves can alter markedly within a few hours after they enter a stream. Nykvist anaerobically leached samples of *Alnus glutinosa*, *Fagus sylvatica*, and *Quercus robur* leaves and found that after 24 hours' leaching *Alnus*

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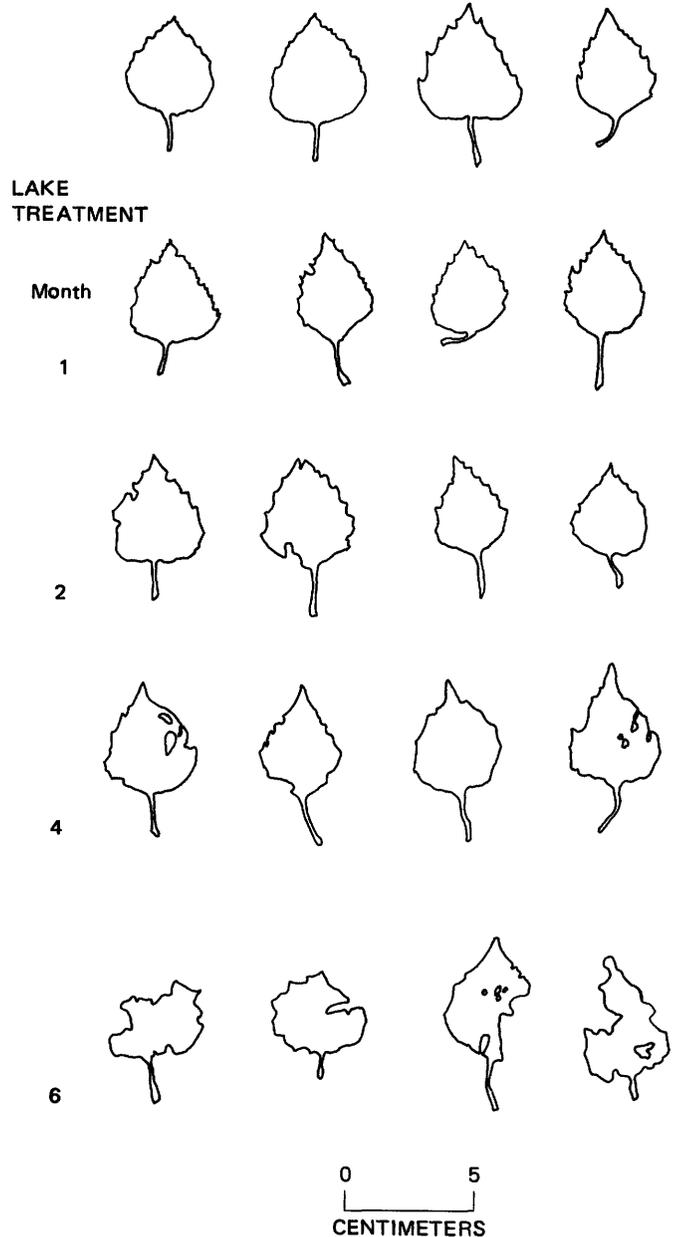
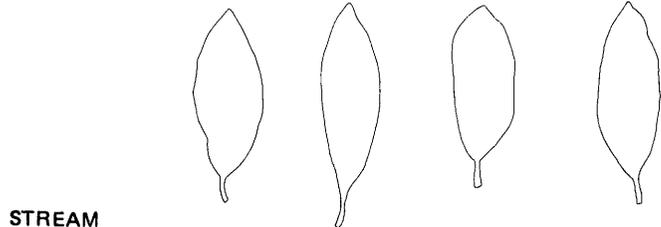


FIGURE 34.—Outline of *Betula pubescens* leaves showing progressive lamina loss in lake-bottom environment. After 8 months, only fragments were left.

had lost 12 percent of its dry weight as soluble organic substances. In contrast, *Fagus* had lost only 3.8 percent and *Quercus* 7 percent. Water-soluble inorganic substances lost after 1 day of leaching amounted to 1.3 percent dry weight for *Alnus*, 1.1 percent for *Fagus*, and 0.9 percent for *Quercus*. Most of the inorganic sub-

stances 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

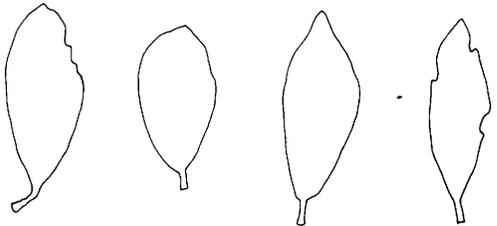
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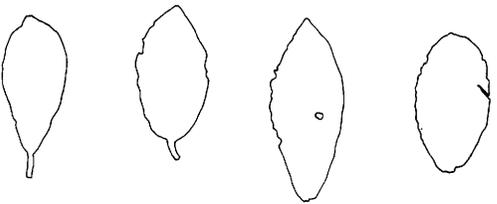
STREAM TREATMENT

Month

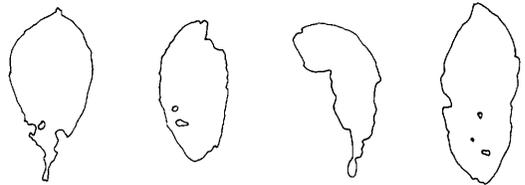
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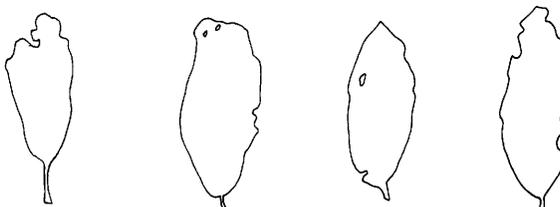
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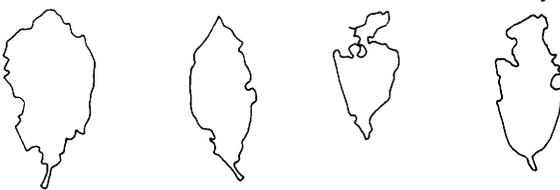
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6



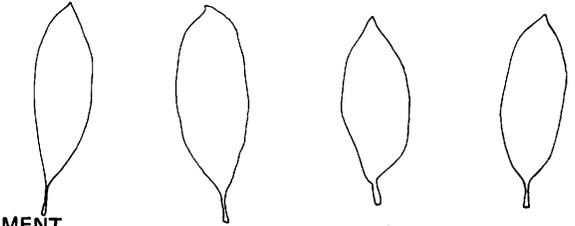
8



0 5
CENTIMETERS

FIGURE 35.—Outline of *Salix cinerea* leaves showing gradual lamina loss under conditions of stream environment.

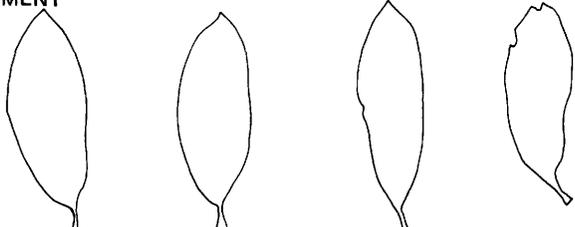
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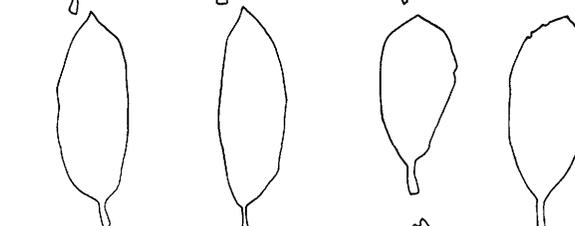
LAKE TREATMENT

Month

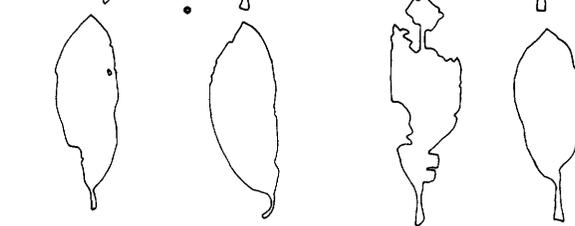
1



2



4



6



8



0 5
CENTIMETERS

FIGURE 36.—Outline of *Salix cinerea* leaves showing area of lamina loss from exposure to lake-bottom environment.

percent of the dry weight in the form of water-soluble organic substances after 1 day's leaching. For *Quercus* the increase was 6 percent; for *Alnus* only 0.2 percent. For inorganic water-soluble substances, grinding gave an increased loss of 0.3 percent for *Fagus*, 0.2 percent 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 released only when the leaf is extensively damaged. It is known that tannins, in the insoluble condensed form, occur in large amounts in *Fagus* and *Quercus* and that they have antifungal properties (Benoit and others, 1968; 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 presumed to be important.

Mechanical

Microbiological activity clearly affects the mechanical strength of leaves. Although it cannot be denied that with most species the loss of mechanical strength is the result of both invertebrate feeding and microbiological breakdown, the example of *Fagus sylvatica* illustrates loss without any sign of invertebrate attack being evident. *Fagus* shows little sign of invertebrate attack even after being exposed for 8 months in either lake or stream environment (fig. 27–28), but results of the rolling fragmentation experiment (figs. 37–43) show that loss of mechanical strength, even in this apparently resistant species, is considerable (fig. 40).

Most species appear to exhibit a higher rate of degradation in the stream environment than in the lake. This is perhaps most clearly shown in the case of *Alnus* (figs. 31 and 32). Examination of the type of destruction suggests that the cause 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. 29 and 30). As

the leaves become less strong, the fluid forces acting on the stream nylon cages caused successively greater fragmentation.

Mechanical fragmentation, like biological breakdown, is to some extent influenced by leaf structure and form. *Salix cinerea*, for example, has a strong midrib; typically, the lamina breaks up, but the pieces remain attached by means of the midrib. *Fagus* seems to be destroyed by random attrition, and in *Quercus* the lobes tend to break off, and the remaining lamina is fragmented, although as in *Salix*, the midrib tends to hold the pieces together. *Alnus* tends to tear rather than break clean like *Fagus* and, though 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, 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 the areas of the whole leaves follow a normal distribution, a bimodal distribution is produced, one peak composed mainly of the fragmented pieces, the other of the larger remains. This pattern can be seen in both *Fagus* and *Quercus*, illustrated in figures 37–39, despite the slightly different forms of their fragmentation. The complex nature of the curves limits the use of such statistics as the median and mode; the measures of fragmentation presented in figures 40–43 are based on average fragment area. It should be pointed out that these estimates are probably higher than the actual numbers because, for practical purposes, a lower limit had to be put on the size of fragments to be counted after rolling. This lower limit was chosen to be 25 mm². 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 exerted on a piece of leaf smaller than 50 mm² were insufficient to break it, but further microbiological attack would probably lead to greater destruction.

Chaney and Sanborn (1933) considered a thin leaf to have only half the chance of a thick one for entering the fossil record, all other things being equal. To test this theory, Ferguson (1971) cut discs of fresh leaves from 11 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 alone, without substantial microbial preconditioning, contributes much to the probability that a leaf will enter a depositional envi-

ronment in a recognizable form. The results of experiments with whole fresh leaves show that they are more resistant to fragmentation than leaves exposed to microbiological attack. Unless the leaf is exceptionally

large (or small), leaf size and thickness are not likely to be as critical in determining the preservation potential of a leaf type as the rate of microbiological degradation. Cuticle thickness is commonly proposed as a major

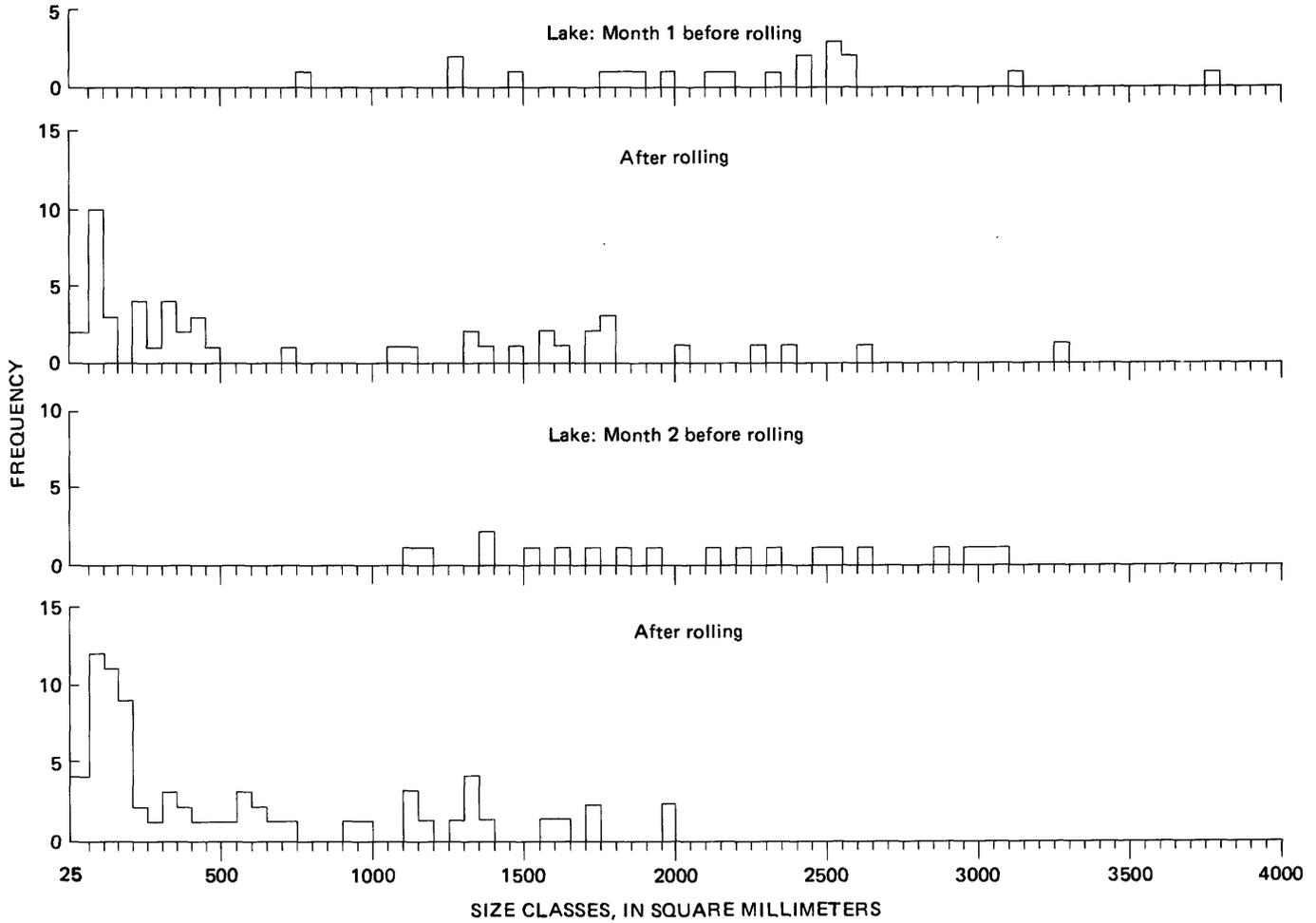


FIGURE 37.—Size distributions of whole leaves of *Fagus sylvatica* before rolling and fragments after rolling.

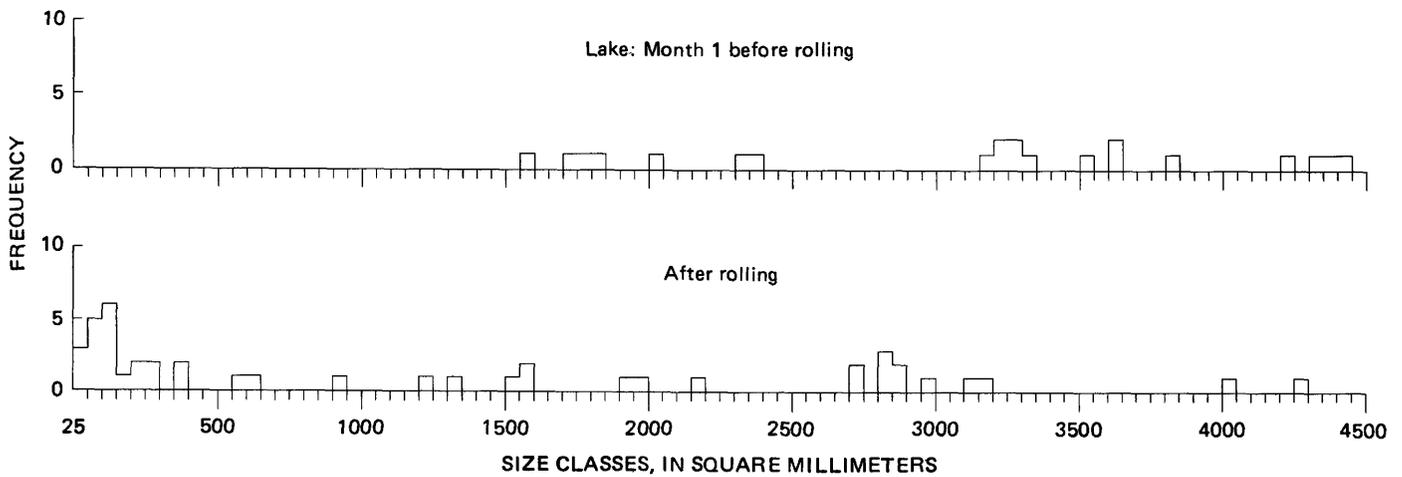


FIGURE 38.—Size distributions of whole leaves of *Quercus robur* before rolling but after 1 month in lake and fragments after rolling.

factor in 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), but it is not necessarily such an effective barrier to the microbiological colonization of the leaf tissues as is sometimes assumed. Where the cuticle is thick, it is commonly left intact even after the rest of the leaf has been destroyed. An 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; all "whole" *Ilex* leaves recovered from the Silwood deposit were in this form. The cuticle of the upper surface of *Quercus* leaves was commonly left intact after an 8-month exposure to the lake environ-

ment. DeVries and others (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. Destruction of the leaf material may take place from the inside and not externally. More extensive cuticle degradation may be prevented by the external coatings of extremely resistant waxes (White, 1933).

It was noted that many leaves present in the Silwood stream become coated with a layer of sediment within 1 or 2 weeks of entering that environment. This encrustation, fully discussed in another paper (Spicer, 1977), may limit external microbiological attack.

Because most fragmentation occurs after some mi-

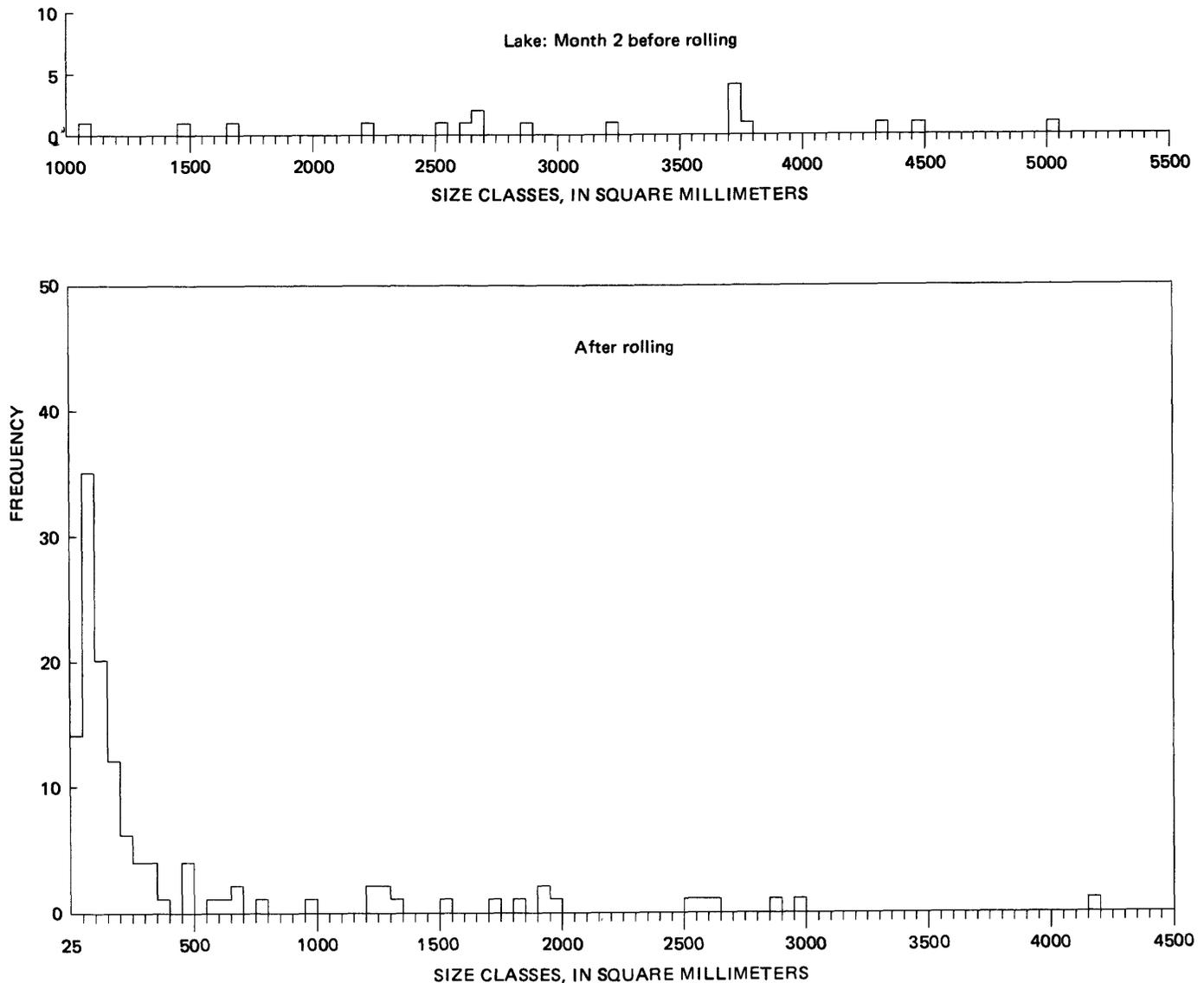


FIGURE 39.—Size distribution of *Quercus robur* whole leaves that had been on lake bottom for 2 months and fragments produced by rolling the leaves.

crobiological breakdown of the tissues has taken place, fragmentation during the floating period will be minimal. Consequently, it is not until after the leaf becomes saturated and is transported in suspension or as part of the bedload that the main process of fragmentation begins. Floating times of as little as 2 or 3 days may mean that some leaves are transported great distances before they begin to be fragmented. These leaves may, depending on the magnitude of the source, 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 recognizable is determined by the fragmentability of the leaf. The five species investigated from the Silwood environment can be placed in an increasing order (from top to bottom) of resistance to biological breakdown as follows:

- Alnus glutinosa*
- Salix cinerea*
- Betula pubescens*
- Quercus robur*
- Fagus sylvatica*

It is not possible at this time to extrapolate these findings to other taxa, even to species of the same genera. More work is required to identify the characteristics of a leaf that determine its susceptibility to breakdown. These characteristics, whether physical or chemical, would, we hope, be those that may be identified in the fossil record.

The differential destruction of leaves during water transport depends on an interplay between potentially destructive environmental conditions and the species-dependent characteristics of the leaves that affect the rate of degradation.

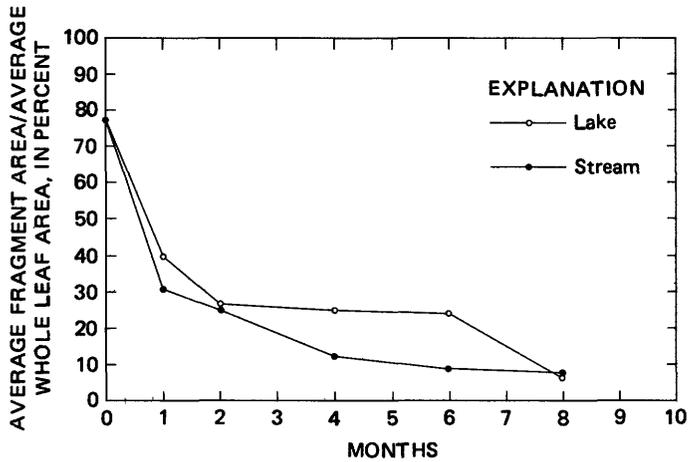


FIGURE 40.—Degradation of *Fagus sylvatica* leaves in rolling experiments after exposure to lake and stream environments for various periods of time.

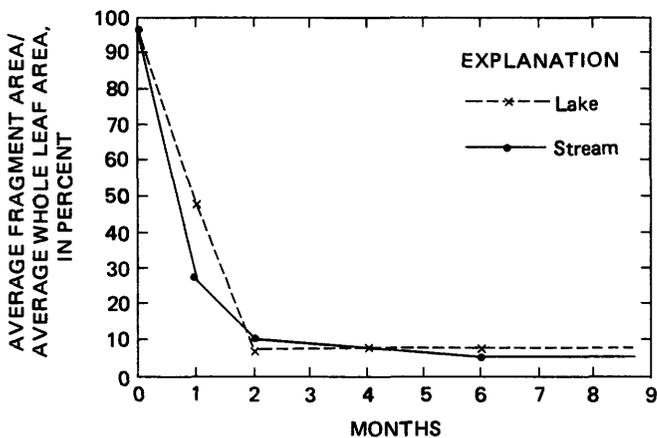


FIGURE 41.—Degradation of *Quercus robur* in rolling experiments after exposure to lake and stream environments for various periods of time.

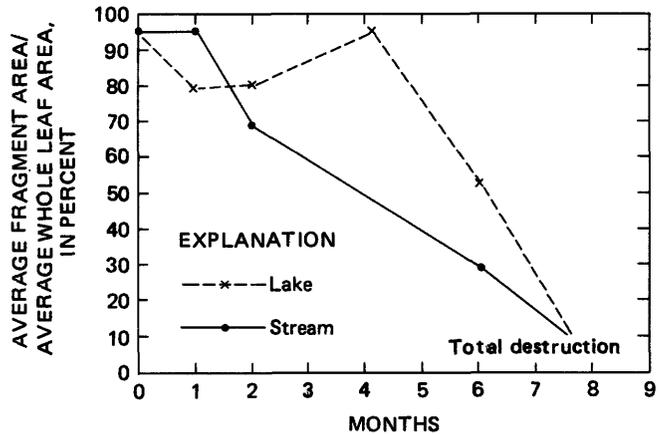


FIGURE 42.—Degradation of *Betula pubescens* in rolling experiment after exposure to lake and stream environment for various periods of time.

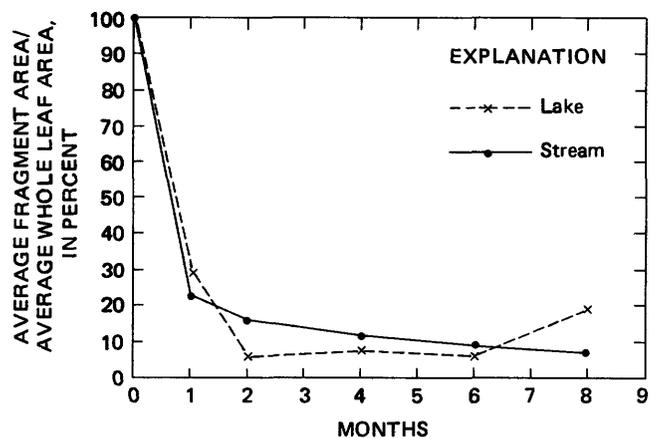


FIGURE 43.—Degradation of *Salix cinerea* in rolling experiment after exposure to lake and stream environments for various periods of time.

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. Variations in the concentration of leaves relative to sediment are used as a basis for distinguishing between assemblages or paleosuccessions (Krasilov, 1969). These fluctuations in plant-fossil concentration may not necessarily be a function of the source vegetation, and therefore the restriction of an investigation to well-defined plant beds may give only limited paleoecological information. As a preface to considerations of sampling in fossil-plant deposits, it is pertinent to examine the plant/matrix depositional relations in more detail.

The rate of leaf deposition, R_l , at any given point on a sedimentary surface can be expressed as

$$R_l = l/\delta t, \quad (1)$$

where 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 can be regarded as constant. Similarly, the sediment deposition rate, R_s , can be expressed as

$$R_s = s/\delta t, \quad (2)$$

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 can be expressed as the leaf:sediment ratio:

$$K = \frac{l}{s} \quad (3)$$

Expanded to include the leaves from the various component species ($a, b, c \dots n$) of the source vegetation, this expression is

$$(R_{la} + R_{lb} + R_{lc} \dots R_{ln})/R_s = \sum_1^n R_{ln}/R_s \quad (4)$$

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

A vertical section through horizontally bedded sediments containing fossil leaves presents a series of bed-

ding planes with varying 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 considered. At 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

$$l = \int_{t_0}^{t_z} (l/\delta t)\delta t \quad (5)$$

or

$$l = \int_{t_0}^{t_z} R_l \delta t$$

and expression (2) becomes

$$s = \int_{t_0}^{t_z} R_s \delta t \quad (6)$$

by integrating between (time) t_0 and (time) t_z , the beginning and end of the depositional period.

Clearly, the smaller the interval $t_z - t_0$ is, the better the resolution obtainable in the analysis of the deposit. Although practical considerations dictate $t_z - t_0$ cannot be infinitely small, loss of resolution and sensitivity in sampling can be minimized by employing the concept of the sedimentation unit proposed by Otto (1938). The sedimentation unit is defined as "that thickness of sediment which was deposited under essentially constant physical conditions." By definition and under ideal conditions, then, if such a thickness of rock is sampled, the relative rates of leaf and sediment deposition have remained nearly constant during the period of deposition, and no loss of resolution will be incurred during sampling. Samples including part of one sedimentation unit and part of another should be avoided. The words "essentially constant" do not preclude the existence of linear or cyclic trends of sedimentation, which, if present, result in changing rates of deposition. Such trends can be identified and allowances made for them during sampling.

The internal structure of a sedimentation unit (individual laminae) is considered by Otto to be the result of erratic perturbations in the transport system and related to "nonassignable" causes. Jopling (1964) pointed out that little is known of how laminae form, but it may be under a wide range of flow conditions, including uniform and steady-state regimes. Clearly the term "essentially constant" must be interpreted somewhat loosely until the mechanisms of lamina formation are better understood. Nevertheless, the concept of the

sedimentation unit is a useful one in the context of defining the framework for quantitatively sampling plant fossils.

Two possible causes for the variation of leaf concentrations, K , between samples are physical conditions and source of leaf material. The primary source of variation must come from the differing physical conditions (hydrodynamic variables and variables of sediment type and availability) that define the sedimentation unit. For leaves being transported by the same medium as the inorganic sediment grains, these conditions will determine sorting, which will inherently affect the value of K .

The second cause of variation, the source of the leaf material, is dependent on the distribution of species within 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 can sometimes be overcome.

THREE-DIMENSIONAL STRUCTURE OF THE SILWOOD DELTA

In order to determine the three-dimensional structure of the Silwood delta, 22 7.5-cm-diameter cores were taken at the positions shown in figure 10 using the assembly (fig. 11) and procedures described under "Coring Procedure." Diagrams of the cores so obtained are shown in figures 44-46. All cores were taken in that part of the delta formed subsequent to its partial drainage in 1957 to construct the present outlet weir. Alder overgrowth of older parts made coring impossible.

PLANT REMAINS

The uppermost part of all cores (with one exception), though semiliquid, exhibited high concentrations of leaf material (leaf bed 1), in some cores admixed with small quantities of coarse silt. Many of the leaves showed signs of both mechanical and biological degradation. Leaf bed 1, though of variable thickness, never extended more than 0.2 m below the sediment surface. The core taken in 0.45 m of water (core DF1, fig. 45) lacked a concentration of leaf material at the top of the core, indicating that at this water depth on the delta foreset slope leaf deposition was minimal. Below 0.2 m, the occurrence of leaves in the cores became rare to 0.7-0.8 m, where another concentration of leaves (leaf bed 2) was encountered. The leaves of bed 2, in contrast

to bed 1, typically showed signs of extensive biological degradation but little evidence of mechanical damage. In leaf bed 2, some 0.2-m-thick, pellets of inorganic sediment were interspersed with leaf remains. These pellets, though widespread laterally, occurred only at this depth (see section entitled "Inorganic Sediment").

In many cores, rootlets were found in growth positions associated with, and below, leaf bed 2, commonly extending down to a dense layer of well-preserved (predominantly *Alnus glutinosa*) leaves overlying, in some cores, a layer of sand. Although leaves were usually not common in the sand layer itself, twigs and *Fagus* cupules were occasionally found. Immediately below the sand layer was a fourth concentration of leaves, somewhat poorly preserved compared with those overlying the sand. Below this leaf bed, leaf remains became rare; the only macroscopic evidence of megaplant remains was layers (not more than 0.1 m thick) of unidentified fibrous plant material.

It was not possible to analyze quantitatively the species distribution of leaves between the cores, but 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.

INORGANIC SEDIMENT

The uppermost centimeter of sediment on the delta, orange brown in color, consisted of flocculent ferric hydroxide admixed with a small silt-size quartz fraction. Much of the silica of this surface sediment was in the form of diatom frustules, commonly *Navicula* sp. The flocculent nature of the sediment precluded any meaningful measurement of settling velocity or grain size, but the bulk of the flocculated sediment had a settling velocity much less than that of most of the plant material.

Large areas of shallow-water delta sediment were stabilized by a prolific growth of blue-green algae belonging to the Oscillatoriales. The ability of these filamentous algae to migrate toward light prevented the burial of the colonies by subsequent sediment deposition. During periods of rapid photosynthetic activity, large gas bubbles formed that became trapped among the filaments. Consequently, areas of the algal mats became buoyant and floated off into deeper water, where agitation by wind-generated turbulence of the lake waters shook the bubbles free, leading eventually to the sinking of the algal/sediment pads. Any sorting of sediments that might have occurred as a result of physical processes of deposition tended to be destroyed.

The upper oxidized layer of the sediment had a pH of 6.8 (table 5), and no crystalline iron minerals were detected by X-ray diffraction studies. Most stream and

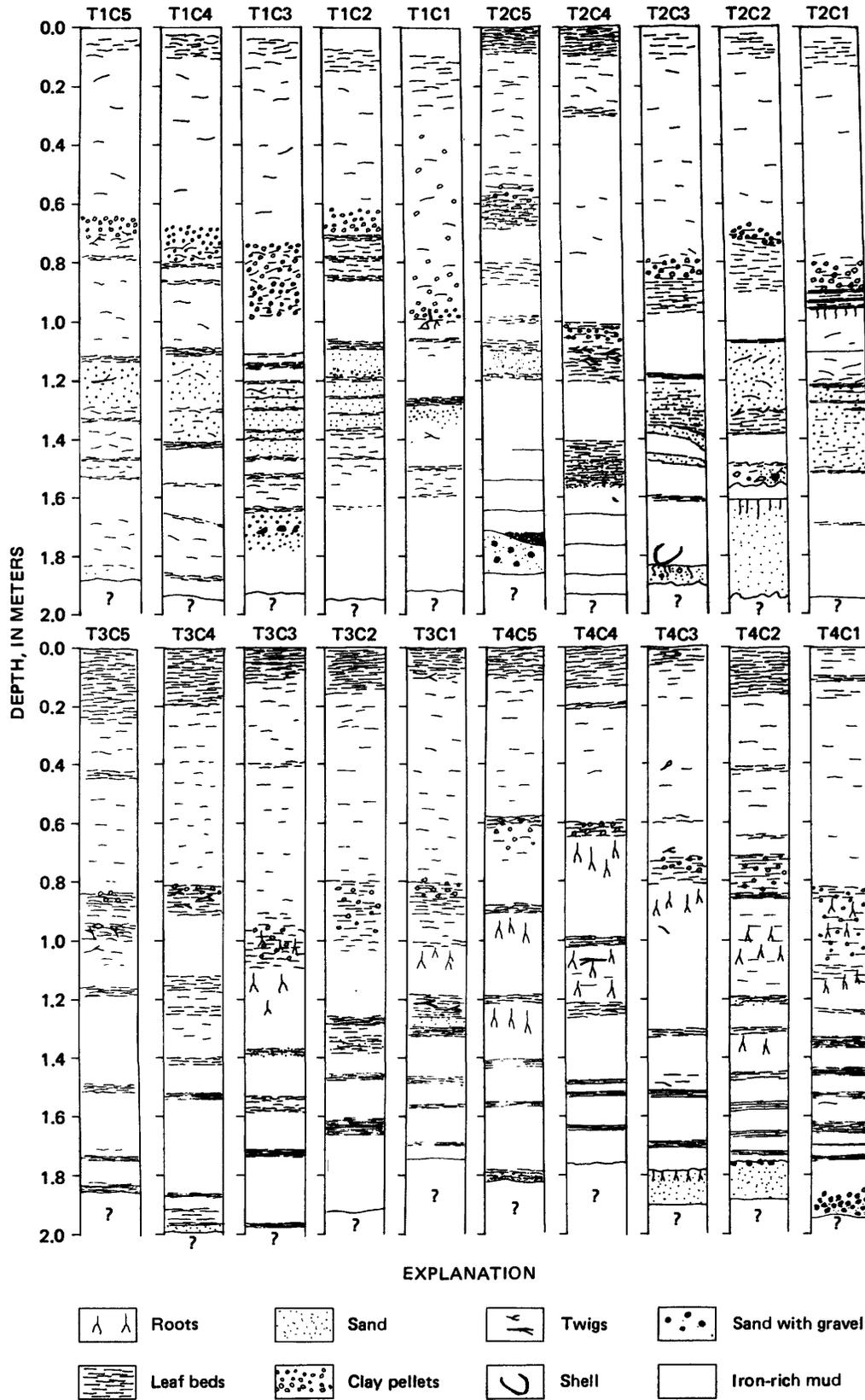


FIGURE 44.—Cores taken from delta in locations shown in figure 10.

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

Approximately 1.0 cm below the surface of the sediment, the color changed from orange brown to black, indicating a change from ferric to ferrous iron. No *Sphaerotilus* or diatom frustules were found in the black sediment of the cores, and in only a few cases were the degraded remains of blue-green algal sheaths

present. The sediment was extremely fluid to the depth of the second leaf bed (approximately 0.8 m), where it became gelatinous. This change in consistency was not associated with any visible differences in sediment

TABLE 5.—Water content, ferric ion concentration, pH, and Eh of the Silwood delta sediment as sampled from a core taken in the Typha bed

Depth (meters below sediment surface)	Percent water loss on drying at 80°C	Percent Fe ⁺⁺⁺ by weight of dried samples	pH	Eh (mV) × 100
0.0	-----	-----	6.8 (stream)	+1.25
.2	83	26.9	7.00	-4.80
.4	85	28.1	7.4 ± 0.2	-4.95
.6	87	36.1	7.00	-6.00
.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	-----	-----

¹Incomplete digestion.

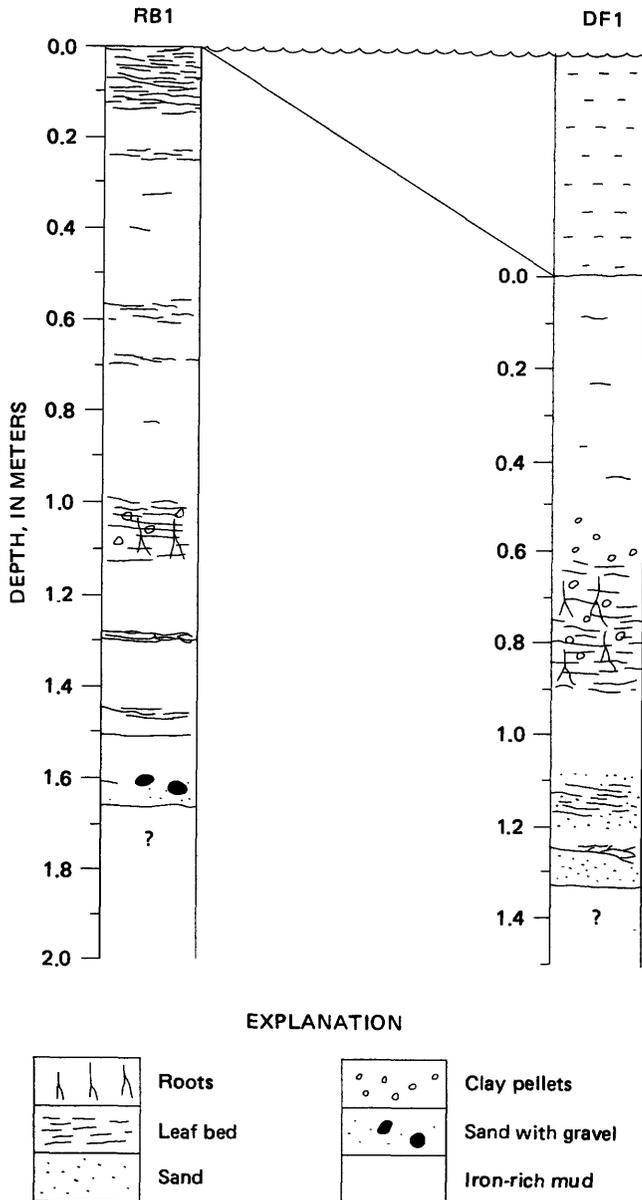


FIGURE 45.—Two cores taken from Silwood delta. Core RB1 was taken close to *Typha* bed, core DF1 on prodelta slope, at locations shown in figure 10.

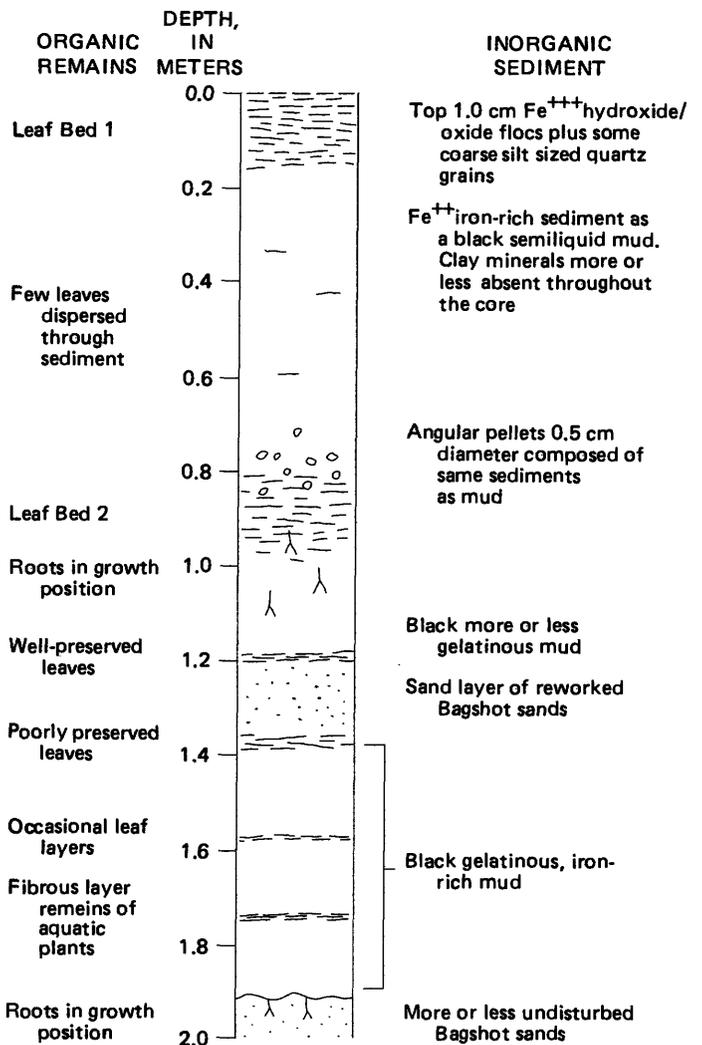


FIGURE 46.—Hypothetical core that summarizes vertical structure of delta.

composition or any large drop in the water content (table 5). X-ray diffraction analysis shows 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 in doubt, but they may be derived from the subaerial deltaic sediments. When the lake was partially drained for some time during the reconstruction of the weir overflow in 1957, the delta surface may have partially dried out. The sediment, once dry, was observed to remain as hard angular pellets that would not redisperse on wetting. It is therefore likely that partial drying of the delta surface may be the origin of the pellets. When the lake level rose again 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, where 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. X-ray diffraction and optical examination indicate that its mineral composition is similar to that of the Bagshot sands; it seems likely, then, that the sand body was derived from erosion of the streambanks during flood conditions. The Bagshot sands were usually encountered at a depth of about 2.0 m and in some cases contained the remains of small vertical roots.

INTERPRETATION OF 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 leaves transported by the stream distributaries, commonly mechanically fragmented.

Leaf bed 2 probably represents deposition of organic material on the lake bottom. The biological degradation of this material in the area from which the cores were taken was probably almost total under normal conditions, but the comparatively rapid deposition of the deltaic sediments arrested this process before it had gone to completion and consequently some of the leaves were preserved. The roots among leaf bed 2, and extending below it, are probably the remnants of aquatic plants that were growing on the lake bottom. The leaves constituting leaf bed 2 were unlikely to have been derived from leaf bed 1 by sinking down through the unconsolidated sediment, as leaves placed on deltaic sediments in the laboratory and left for periods as long as 2 months did not show any tendency to sink.

The sand body undoubtedly represents a period of abnormally rapid deposition. As the sand was being deposited, litter from the surrounding vegetation must have been 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, and as this settled out, it rapidly buried the newly deposited leaves and other organs. Well-preserved *Alnus* leaves are found in the cores only in this position, underlain by coarse sediments and overlain by fine.

Below the sand layer is another leaf bed that, like leaf bed 2, represents 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 m, the lake sediments are found to directly overlie the Bagshot sands. In a few cases, the remains of a soil horizon occasionally containing vertical roots overlie the Bagshot sands. These roots are interpreted as belonging to the original vegetation that grew in the valley before it was flooded.

A GENERAL MODEL OF LEAF DEPOSITION IN A FLUVIOLACUSTRINE ENVIRONMENT

The information presented here is of limited value if it cannot be related in principle to processes that are likely to have operated in the past. While biological factors may change significantly with time, the physical and chemical processes of transport and deposition are likely to be less time dependent. To be valid over geologically significant periods in the past, generalizations derived from the Silwood study should be as independent as possible of biological variables.

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 has critical paleoecological implications.

The relative rates of leaf and sediment deposition were used (p. 40-41) to show how variations in leaf concentration within a volume of sediment might well reflect both the hydrodynamic properties of the plant material in relation to the inorganic sediment grains and more significantly the distribution of the source vegetation. Utilizing this approach, it is now possible to give an example of how such parameters affecting the variations of the leaf: sediment concentration ratio (K) may be analyzed.

Consider the representation of figure 47. 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 (Smith, 1975) will be formed. 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 or not a bed density current is set up, 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, the leaves from the surrounding vegetation either fall, or are blown, onto the surface of the lake, where they may float for various periods of time. During this time, if the leaves are free from the influence of any inflowing streams, they will be distributed directly by wind or wind-generated water currents. Most leaves, fruits, and seeds will enter the water close to the banks and may be trapped by aquatic vegetation such as reeds or *Nuphar* sp. pads. As the plant material sinks to the bottom, it will gradually form a lake bed, rich in organic material, and provided organic input exceeds degradation, a potential plant megafossil bed will form that reflects the composition of the local vegetation (H. H. Birks, 1973).

When there is no prevailing wind direction, the deposition along any line running parallel to the shoreline of leaf material by means of direct aerial transport from the local vegetation is likely to be nearly uniform, because all points along the line are

equidistant from the source. The schematic (fig. 47) depicts a vertical section through the delta parallel to the shoreline and normal to the delta front. The relative sedimentation rates are represented by the length of the two vectors normal to the sediment surface. As in the Silwood situation, it is assumed that most of the inorganic sediment has a settling velocity less than that of waterlogged plant remains.

The rate of inorganic sedimentation in the lake is very low relative to that of the "rain" of local plant material. 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 prodelta slope, R_s has begun to increase, while R_l , dependent on the local vegetation, remains essentially constant such that $K \approx 1$. At point *C*, on the prodelta 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, leaf fragments transported as bedload material and both organic and inorganic sedimentary particles with high settling velocities collectively settle out in the even higher water energies acting at the top of the foreset slope. At Point *E*, then, $R_l > R_s$, and again

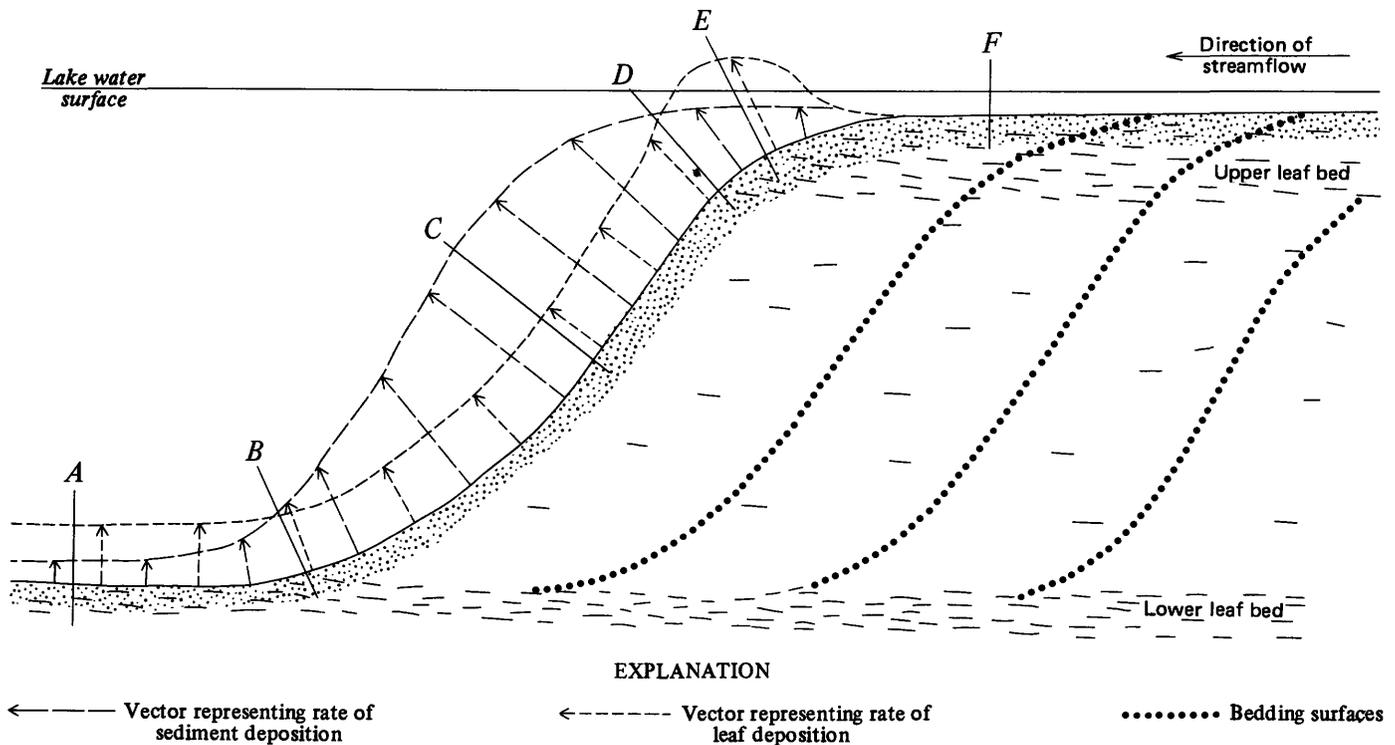


FIGURE 47.—A diagrammatic representation of leaf deposition in a freshwater delta environment. See text for explanation. See text for discussion of points A-F.

a concentration of leaves is produced. At point *F*, within the stream channel, deposition and erosion are nearly balanced, although leaf input 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; although there is evidence to suggest that the breeding cycles of many aquatic invertebrates is linked to periods of rapid organic input (Petersen and Cummins, 1974), the population of leaf-degrading organisms present in the depositional environment may 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 predominantly in the lower leaf bed, the species growing at more distant locations in the upper bed. Not only will the species composition differ but so also the type and extent of degradation. The transport of the local species to the surface of the lake water will be mainly by wind and mechanical damage therefore minimal. In the lake-bottom waters, rich in organic material, biological degradation could be considerable and would be detectable by the characteristic rounded holes of invertebrate attack and the loss of intercostal 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 evidence of biological degradation. Repeated reworking of this upper-leaf bed as the distributaries wander laterally over the delta surface will further mechanically degrade the leaf remains. Because not all the leaves coming down the stream will be at the same state of waterlogging on reaching the stream mouth, any sorting effects due to the various hydrodynamic properties dependent solely on fragment size or thickness are not likely to be observed.

Observation in the Silwood stream showed that a small fraction of the leaf population (most likely to be whole for the reasons discussed in the section "Leaf Degradation") 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. This distinct-species component of the lower-leaf bed, although small, 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 condition 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 relative to leaves of *Fagus* and *Quercus*. In this situation, it appears that one local species was quickly removed from the potential fossil record, resulting in an overrepresentation of the distant component in the lower leaf bed. Such conditions need not, of course, apply to all situations. There is no evidence to suggest that susceptibility to breakdown is a general feature of all riparian plants; different components of a flora may be either underrepresented or preferentially preserved in a fossil deposit.

Clues as to which floristic components were easily degraded in the past can be obtained by examining the leaf/sediment relations. 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 penetrated by the cores (figs. 44–46) was formed. After deposition of the sand, a great amount 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. Only under these conditions were well-preserved *Alnus* leaves 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 input of organic matter. 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* the partial pressure of oxygen in the atmosphere, *pt* the pressure at which the concentration of gas at time *t* in the water would be in equilibrium, and α a coefficient termed the entrance coefficient (Hutchinson, 1957, p. 588). It is evident, therefore, that the rate of movement of oxygen across the air:water interface is dependent on the area of that interface. As the area of the lake surface diminishes before the advancing delta, the total oxygen exchange between the atmosphere and the lake drops. At the same time, the ratio between the perimeter length and the lake area increases, giving rise to an effective increase in organic input per unit area of the

lake surface (Rau, 1976). A combination of these factors leads to a thickening of the layer of organic matter on the lake bed. It is unlikely, however, 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 (Kaushik and Hynes, 1971).

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. It does indicate that the possible effects of the shape and size of a depositional basin on floral representation must be considered.

In the deposition model (fig. 47), the upper leaf bed was seen to originate from differences in the hydrodynamic characteristics of leaves 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 megaremain, has already been shown to be wide and unpredictable, but most 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. An upward-coarsening sequence, typical of many large fluvio-marine deltas (Selley, 1971), is commonly less well developed in freshwater deposits owing to the rapid dissipation of energy in the turbulence caused

when river waters meet static lake waters of similar density. 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.

In order to examine the consequences of the leaf-deposition model just described, let us consider the infilling of a lateral lake by the progressive advance of deltaic sediments (fig. 48). The bottommost lake deposits might reflect the sediment load of the major river during flood, but subsequently the basin would steadily fill with megaremain from the local flora together with a little inorganic sediment. Evidence of intermittent flood events might be preserved. As the delta advances across the lake, the upper and lower leaf beds are formed as described. Initially, the upper lake is maximal in area and well oxygenated. Under such aerobic conditions, the organic input to the lake is rapidly broken down and the only local leaves preserved are those that become covered by the deltaic deposits before they are destroyed. At the very beginning of deltaic sedimentation, immediately after the formation of the lake, there would be only one deposit rich in organic material, but as the delta begins to form, so will the upper leaf bed. Initially, the lower leaf bed might be very thin, whereas the upper leaf bed would be, by comparison, rich in species growing upstream.

As the delta advances, its surface becomes successively colonized by various plants, and a hydrosere develops. Some of the leaves from the distant species are now filtered out by new vegetation, which contributes

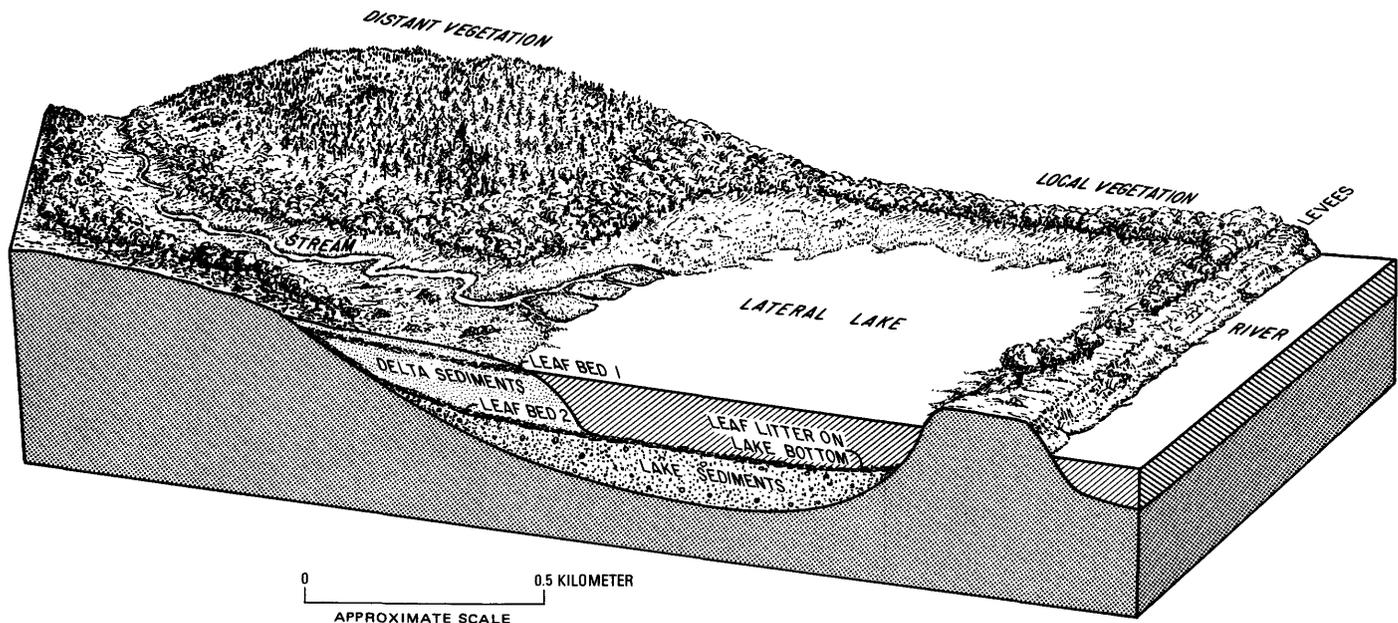


FIGURE 48.—Schematic drawing of leaf-bed formation in a lateral lake.

its own remains. 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 upper leaf bed may also thicken by secondary contributions of the hydrosere vegetation, which, in species composition, may resemble the lakeside communities.

The final condition of the basin is shown diagrammatically in figure 49. A vertical section through the completely 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 species composition of the assemblages converge (fig. 49B).

If the basin is then vertically sectioned normal to the infill direction (fig. 49A), the bottom leaf bed may exhibit a thickening toward the basin margins (although the bulk of the finely divided, unidentifiable organic matter may accumulate in the bottom of the basin; Rickett, 1921), while the upper leaf bed will vary in composition laterally depending on the pattern of the distributaries. 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 remains of the vegetation that originally grew in the now-drowned valley.

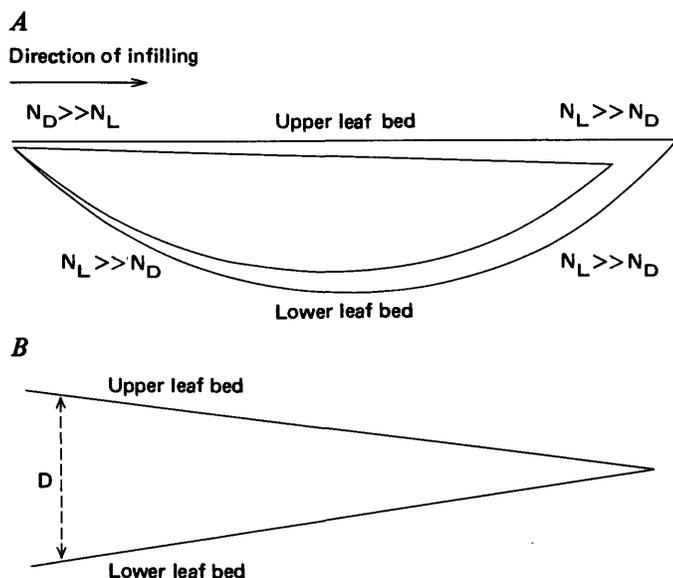


FIGURE 49—Longitudinal vertical sections through a completely infilled lake basin. A, Species composition of upper leaf bed changes from one dominated by a large distant component N_D , in early stages of infill to an assemblage dominated by local components of flora N_L , as a hydrosere develops on compacted delta sediments. 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 situation is likely to be only rarely preserved intact and recognized in consolidated deposits. The pattern of two leaf beds, separated by comparatively unfossiliferous fine-grained sediment, is common, and this model illustrates one way by which such a structure may form. Knowledge of other ways, or their paleoecological implications, may come from work 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 three-dimensional structure of the deposit and the relation between the two leaf beds and the surrounding inorganic sediments are determined, then useful paleoecological information will 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 the distribution of vegetation types over the land surface surrounding the basin of deposition. Conversely, lateral changes in species composition within a single continuous leaf bed may reflect a change in vegetation with time as, for instance, in the development of a hydrosere.

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, "Target population II," will be derived.

The degree of accuracy achieved in describing the Target population I 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 population I 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. The nature of the rock matrix, combined with the three-dimensional nature of a sedimentary deposit, imposes certain constraints 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 (in the sense of Orloci, 1968a) within the sampled community, cannot always be met when sampling fossil plant assemblages for the following reasons:

(1) Restrictions on the amount of material available for sampling—The fact that any deposit is exposed for sampling by the paleoecologist is usually the result of partial removal of the original fossil population. The initial exposure is often made by natural erosion but may also be the result of activities of man, for example, quarries or road cuts. Some of the deposit, moreover, may be inaccessible because it is covered by large amounts of other rock in the form of scree, fallen boulders, or slumping.

(2) Weathering.—Of the accessible deposit, large volumes may be differentially weathered, and this may lead to the selective destruction of some of the component fossil species.

(3) The splitting properties of the rock matrix.—Clearly any sedimentary rock that cleaves parallel to the bedding will favor the exposure of entombed fossils, since most remains are deposited, or distorted by compaction; consequently, their plane of largest area is parallel to the bedding surface. A large number of factors, including the presence of organic remains, affect the splitting properties of rocks.

In all but the most homogeneous deposits, the factors given will largely determine the sampling regime, and because 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. 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 analysis and correspondence analysis.

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

STAND SIZE

In the plant ecology, the size of stand is primarily determined by scale within the vegetation, and this is equally critical in the analysis of fossil-plant assemblages. The construction of a species-area (or species-volume) curve to determine a suitable stand size (see Greig-Smith, 1964, p. 151–155, for relevant discussion) has to be based on the portion of the sample population immediately available at the start of sampling. This estimate of stand size may not be suitable for sampling all parts of the fossil population.

The effect of pattern within fossil deposits may greatly influence the choice of size for the minimal or representative quadrat area (Greig-Smith, 1964, p. 155):

“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 mosaic of patches with higher and lower density *** will appear at a smaller quadrat size.”

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 any but the most uniform conditions. Work at Hasty Bank, England, carried out by C. R. Hill, has shown that the choice of stand area, or volume, may in fact have to change with differing lithologies, fossil density, and fragment size. (C. R. Hill, 1974; Spicer and Hill, 1979).

THREE-DIMENSIONAL SAMPLING

The analysis of the distribution of plant remains over a single bedding plane is analogous to investigating vegetation pattern over a land surface, as both may be assessed by 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.

(1) The concept of a bedding plane is not immediately conducive to this type of sampling, because it may not have any physical expression. Sampling over large lateral distances would inherently involve the possibility of sampling across different bedding surfaces.

(2) 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. The required excavation will then encroach upon underlying bedding planes, resulting in the breakdown of the sampling regime.

(3) The splitting properties of the matrix may preclude the exposure of planar stands of sufficiently large area; consequently, the excavation of rock of a finite thickness is inevitable.

Sampling volume rather than area introduces yet further problems. The extension of the boundaries of a stand (sample) in a direction normal to the bedding introduces the likelihood that the rock, including individuals that constitute the stand, was laid down under

changing depositional conditions. As stated, to minimize this problem it is necessary to utilize the concept of the sedimentation unit proposed by Otto (1938). Otto's concept permits heterogeneity in the distribution and abundance of the various species of plant remains without prejudicing the delineation of the unit, because it allows for chance deviations of all sedimentary characteristics about a mean value. Nevertheless, it should be borne in mind that, because we are considering dispersed plant units as sedimentary particles, the gross abundance of plant remains may be used as one of the criteria for defining the sedimentation unit. Other criteria for identifying these boundaries are given in Otto's paper (1938).

After deposition, sediments will become compacted, and this will increase the abundance of plant remains per unit volume of rock. If compaction is uniform, it has little consequence, but such a condition is not always fulfilled. The degree of compaction is likelier to differ from place to place throughout the deposit such that the relation of fossil abundances between stands becomes distorted. Under these circumstances, any statistical procedure that is susceptible to varying interstand abundances in the derivation of floristic ordinations, as in principal components analysis, should not be used.

QUALITATIVE AND QUANTITATIVE ASSESSMENTS OF ABUNDANCE

There has been much discussion in the literature about the use of quantitative and presence/absence (P/A) scores in phytosociological studies. Lambert and Dale (1964) argue that P/A records form a self-contained logical system, whereas 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 differs from Greig-Smith's (1964) view that absence is an extreme of a continuous variable that describes the amount of a species that is present. Orloci (1968b) considers P/A scores as primarily relating to establishment and survival of individuals, whereas quantitative measures of abundance relate more to relative performance. Such concepts are of course meaningless when one is dealing with paleobotanical data derived from allochthonous assemblages, but it is nevertheless necessary to consider from a practical standpoint how the stands should be scored. Whatever assumptions are made regarding the relative merits of quantitative scores, the amount of information contained in P/A scores of a particular species can be measured and compared with that contained in quantitative scores. Subsequent decisions may then be

made on the basis of a pilot study as the the type of scoring system to be adopted in the main investigation. The term information in this context is used in the strictly technical sense and describes a physical property of the data that is related to the likelihood of an observation rather than any intrinsic "meaning." Orloci (1968b) presents a method by which the information content of a suite of observations on a species may be partitioned into two independent components, a presence/absence component and a quantitative component. The loss of information incurred by assessing P/A instead of making quantitative measures of abundance can be measured and its significance tested.

The total information in the i^{th} species of a data matrix (X) (in which rows represent species and c columns represent sites), with x_{ij} representing the value of the i^{th} species in the j^{th} site, may be expressed as:

$$I_i = - \sum_{j=1}^s f_{ij} \ln p_{ij}, \quad (1)$$

where the c observations have been summarized in an s -celled frequency table for each species and the class frequencies and corresponding proportions are given by f_{ij} or p_{ij} such that

$$j = 1, 2, \dots, s, \quad p_{ij} = f_{ij}/c, \quad \sum_{j=1}^s f_{ij} = c, \quad \text{and } p_{ij} = 1/c.$$

The presence/absence component is then given as

$$I_{i1} = -f(x_{ij} = 0) \ln p(x_{ij} = 0) - f(x_{ij} > 0) \ln p(x_{ij} > 0). \quad (2)$$

The quantitative component is then given as

$$I_{i2} = I_i - I_{i1}. \quad (3)$$

Because I_i consistently underestimates the population value, a correction factor $I_i + \Delta_i$ is required where

$$\Delta_i = (s-1)/2 - (2-3s + \sum_{j=1}^s 1/p_{ij})/6c. \quad (4)$$

The sampling variance for I is then

$$V(I_i) = c \left(\sum_{j=1}^s p_{ij} \ln^2 p_{ij} - H_i^2 \right). \quad (5)$$

This last expression differs in two respects from that originally given in Orloci (1968b). The last term o is omitted to correct an error in the paper, and H_i is defined as I_i/c rather than $(I_i + \Delta_i)/c$ to avoid negative values (Orloci, written commun., 1976); the confidence limits are defined by

$$\text{Conf} = 1.96 \sqrt{V(I_i)}. \quad (6)$$

Using this method, it was possible to assess the information content of both the whole-leaf and fragment density data from Silwood delta; the results are presented in tables 6 and 7.

It can be seen that in both cases more information resides in the quantitative component and that in all but the rarer species, scoring on the basis of P/A rather than density would lead to significant losses of information.

It is difficult to make sound generalizations concerning P/A scoring versus quantitative scoring in paleoecology owing to the lack of relevant information. It would not be surprising in many circumstances, however, to find that over single bedding planes, most of the information resides in the quantitative component. The so-called random variation in sedimentary data (Blackith and Reyment, 1971) brought about by the innumerable variables of deposition will tend to make the distribution of any population of sedimentary particles lying on a single bedding surface appear almost homogeneous. On the other hand, a vertical series of samples that cut across different sedimentary units is likely to exhibit more heterogeneity, and therein a larger component of the total information will reside in P/A scores. These intuitive comments remain to be tested.

Unless presence or absence data are 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 unit sample.

Cover—The proportion of a planar unit sample area,

aligned parallel to the bedding, that is occupied by a normal projection onto it of the individuals representing a species form that occur within that unit sample.

The cover definition assumes that the dispersed leaf remains have their surface of greatest area lying parallel to the plane of bedding, and both refer to the potentially measurable parameters of the Target population I. The success of achieving an accurate assessment of species abundance in the Target population I is dependent on characteristics of the sampling method as well as the rock matrix.

To demonstrate this contention, consider a diagrammatic representation of a vertical section through a three-dimensional sample stand, figure 50. 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 of the incorporated fossil material. The actual number of leaves lying within the rock close to this plane was four. Fragmentation of the leaf on the extreme right, however, leads to the exposure of five pieces of material; in this case, then, a 25-percent overestimate 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 percent. The complete exposure of fossil leaves, necessary for accurate cover measurements, is rarely if ever achieved; as a result, underestimation of the Target population I cover abundance is inevitable. Density, on the other hand, may lead to a potential overestimation of abundance if excavation or splitting of the stand surface is not carefully carried out.

TABLE 6.—Fragment density per quadrat

[Information partition statistics calculated using leaf-fragment density data collected from top 2 cm of delta sediment]

Species	Total information	95-percent confidence interval 1.96 V(I)	Presence/absence component	Quantitative component
<i>Alnus glutinosa</i> -----	278.54	11.04	9.75	268.79
<i>Betula pubescens</i> -----	181.05	12.55	41.64	139.41
<i>Fagus sylvatica</i> -----	176.40	24.78	51.86	124.54
<i>Quercus robur</i> -----	216.35	15.71	35.81	180.54
<i>Salix cinerea</i> -----	206.91	37.34	28.51	178.40
<i>Ilex aquifolium</i> -----	151.82	16.13	52.95	98.87
<i>Aesculus hippocastanum</i> -----	53.30	18.01	37.39	¹ 15.91
<i>Acer pseudoplatanus</i> -----	26.39	11.47	26.39	¹ 0
<i>Crataegus monogyna</i> -----	16.29	51.86	16.29	¹ 0
<i>Typha latifolia</i> -----	157.21	19.07	53.83	103.38
<i>Nuphar lutea</i> -----	54.23	58.83	37.39	¹ 16.84
<i>Salix alba</i> -----	40.54	18.35	28.51	¹ 12.03
Total -----	1,559.03		420.32	1,138.71
Percent total --	100		27	73

¹Losses not significant at 95-percent level if presence-absence component replaces quantitative scores for abundance.

TABLE 7.—Whole-leaf density per quadrat

[Information partition statistics derived from whole-leaf density data collected from top 2 cm of delta sediment]

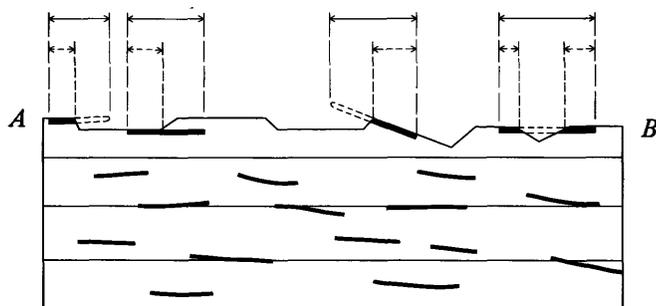
Species	Total information	95-percent confidence interval 1.96 V(I)	Presence/absence component	Quantitative component
<i>Alnus glutinosa</i> -----	150.14	39.89	41.64	108.50
<i>Betula pubescens</i> -----	142.06	9.74	49.31	92.75
<i>Fagus sylvatica</i> -----	98.61	23.49	55.25	43.36
<i>Quercus robur</i> -----	99.27	24.38	52.95	46.32
<i>Salix cinerea</i> -----	183.32	22.89	38.89	144.43
<i>Ilex aquifolium</i> -----	19.10	11.44	19.10	¹ 0.00
<i>Aesculus hippocastanum</i> -----	29.73	13.92	26.39	¹ 3.34
<i>Crataegus monogyna</i> -----	13.20	3.95	13.20	¹ 0.00
<i>Salix alba</i> -----	5.70	8.49	5.70	¹ 0.00
Total -----	741.13		302.43	428.70
Percent total --	100		41	59

¹Losses not significant at 95-percent level if presence-absence component replaces quantitative scores for 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 estimate the exposed cover, because 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 both cover and density are measurements of abundance, they measure different properties of the population, and the meaning of either of them, or the relation 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 therefore likely that throughout a deposit, in particular vertically, variations in plant density will be associated with variations in lithology.

Cover is controlled mainly 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 tend to



EXPLANATION

- ←→ Actual leaf size as would be measured by cover if all the leaf was exposed
- ←- - - - Leaf size as measured by cover estimates
- Lines representing the orientation of bedding planes

FIGURE 50.—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. Leaves, shown in section, have influenced the splitting along A-B but have become fragmented in the process, making density and cover estimates show erroneous assessments of abundance: density overestimates abundance, and cover underestimates abundance.

have a high cover rating from those stands in which it occurs. Species Y 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. 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. 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 results of the delta trap experiments show that long-distance aerial transport selects in favor of small leaves (figs. 18 and 20). The selection of small leaves by aerial transport, which results in the biased representation invalidates cover as an abundance measure because species transported to the depositional site mainly 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. Because the processes that lead to mechanical fragmentation are predominantly those found in fluvial environments, however, the detection of pattern that is linked to fragment density is potentially useful for distinguishing those taxa that might have grown around the lakeside from those that occupied streamside habitats.

While there are clearly arguments both for and against the use of either measure, it would seem from a 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 that density is a more suitable measure of abundance.

PRINCIPAL COMPONENTS ORDINATION AND CORRESPONDENCE ANALYSIS

Multivariate statistical techniques such as principal components analysis (P.C.A.) and principal coordinates analysis (Gower, 1966) have been used for some time in studies of living vegetation (for example, Orloci, 1966). P.C.A. has proved particularly suitable for investigating environmentally dependent patterns that might occur within vegetation where no pattern has previously been suspected. In this context, pattern is used in a broad sense and should be regarded as nearly synonymous with the term "structure" as used, for example, in phytosociology to describe intrinsic properties of a particular data set (see Orloci, 1968b). Although normally presenting a continuum that might be assigned to an environmental gradient, P.C.A., and indeed most ordination methods, will detect discontinuities, and the data will thereby be grouped, if such a clustering is justified. The clustering produced by P.C.A. may then be used as a basis for dividing the vegetation sampled into communities, each exhibiting a more homogeneous structure. Despite a theoretical requirement for linearity of data structure (Orloci, 1975), P.C.A., like many other multivariate statistical methods, is remarkably robust, which means that it will still give a fair result on data not fulfilling this premise. This robustness allows application of such methods to the analysis of plant fossil distributions, where sampling may be subject to constraints of exposure and lithology and where the distribution of the abundances of individuals may depart from normality.

Principal components analysis may be thought of in the following way. If only two species were present in the sample population, the occurrence of these species within a stand (quadrat) would define the position of that stand on a two-dimensional graph, the axes of which represent 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 multidimensional hyperspace. Clearly this only begins to have understandable meaning if the distribution of stands or species can be summarized by projection onto three dimensions or less, but this unfortunately introduces distortion. The distortion may be minimized if the projected axes are aligned with the principal axes of variation within the multidimensional scatter. P.C.A. is a method of detecting these principal axes, or major components of varia-

tion, in data matrices.

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

STANDARDIZATION

Standardization is a widely used technique for transforming the data to allow comparison of variables that have been measured in different units. The transformation of the raw data matrix is achieved by subtracting from each observation the mean of the set of data and dividing by the standard deviation. In this way, a new matrix is derived in which the variables have a mean of zero and a variance of one. Such a procedure, provided that all raw variables had initial variances > 1 , 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; for example, those species with a high variance are divided by a correspondingly high standard deviation. Such adjustment may not always be desirable, but when differences in abundance between stands, which cause fluctuation in variance, are brought about by factors other than those of direct paleoecological significance (for example, differential rates of sedimentary compaction), standardization could be accepted.

Another way of reducing the overall variance in a set of data is by means of a logarithmic transformation. The usefulness of this procedure, which does not alter the relation between species (or stands), is demonstrated by Spicer and Hill (1979) using data collected from a Jurassic plant fossil locality.

PRINCIPAL COMPONENTS ANALYSIS ORDINATION OF THE SILWOOD DELTA SURFACE DATA

Leaf-fragment abundance data from the surface sediment of the Silwood delta (see fig. 8 for sampling positions) were analyzed by PCA ordination using both unstandardized data and data that had been standardized to unit variance. The computer program (Q.P.C.A.), written by A. J. Morton of Imperial College, is based on an iterative procedure (Lawley and Maxwell, 1963) and operates on a half matrix to reduce computer memory requirements.

The plot of the unstandardized principal component ordination (fig. 51) exhibits a tight bunching of most of

the stands on the left of the diagram. Reference to the raw data (data table 1) shows all these stands have relatively low species abundances. It has been pointed out by Orloci (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. In figure 51, the stands plotting apart are those with high species abundances. Axis 1 then appears to reflect variation due to abundance. Such an observation is not new, and indeed is common in P.C.A. ordinations. Axis 2, however, may be assigned, by inspection, to reflect a trend from proportionately high *Alnus* abundances to proportionately high *Fagus/Quercus* abundances.

The standardized data orientation (fig. 52) seems to differ little from that obtained from unstandardized data. Axis 1 is again aligned along an axis of abundance; axis 2 reflects ordering from proportionately high *Alnus* abundances to proportionately high *Fagus/Quercus* abundances. The total variation accounted for

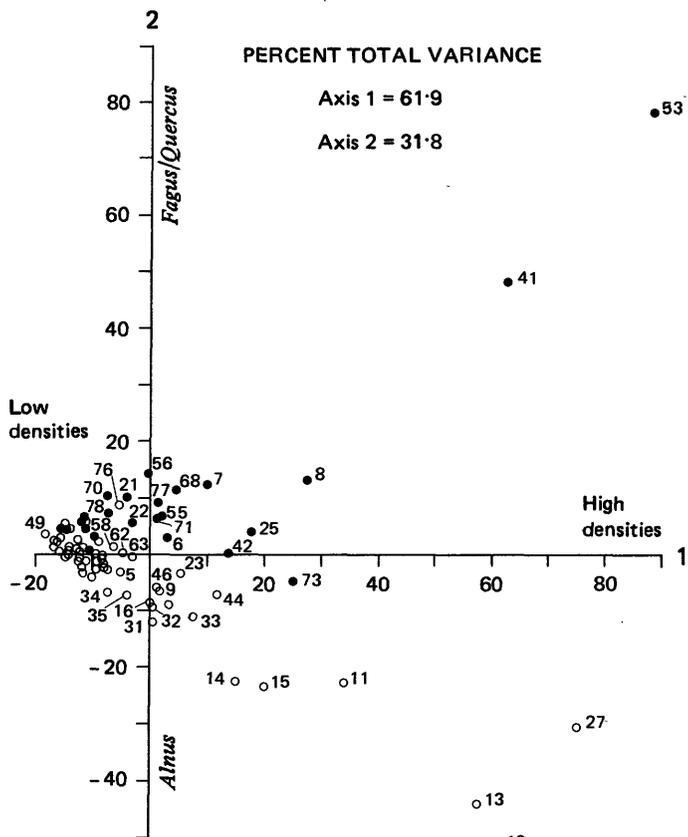


FIGURE 51.—Axes 1 and 2 of a principal components ordination of nine species of leaves occurring in Silwood delta sediments. Ordination based on unstandardized fragment-density data. Numbers refer to quadrat numbers (see fig. 8). Dots represent those quadrats belonging to the *Fagus/Quercus* group as identified by correspondence analysis (fig. 54); circles represent the *Alnus*-characterized group.

by the first two axes of the unstandardized data ordination was 94 percent, whereas that for the standardized was only 52 percent. Standardization has apparently reduced the effectiveness of the ordination. Both ordinations have identified, on axis 2, an axis in the data along which stands may be ordered in terms of the relative abundances of *Alnus* or *Fagus* and *Quercus*.

Successful as P.C.A. ordinations are in presenting trends such as floristic gradients, the method itself is constrained by a number of drawbacks. Unstandardized P.C.A. ordinations are not corrected for species abundance, and the results show that the rarer species have a smaller axis score than the more abundant species even though their distributions throughout the sampled population may be similar. This introduces problems when dealing with fragmented plant fossils that may have been only parts of a single living entity. Naturally occurring associations between organs would not be detected, because, for example, flowering parts would normally be considerably rarer than leaves.

In a stand ordination, this characteristic of P.C.A. has even more disturbing consequences. If the abundance of fossils within a unit volume of rock is noted,

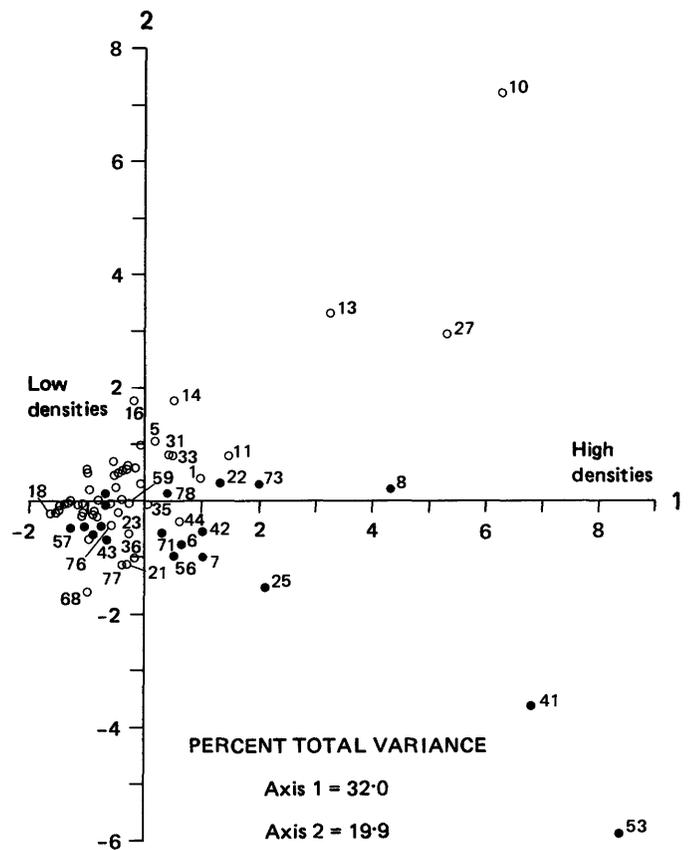


FIGURE 52.—Ordination similar to figure 51 but based on data standardized to unit variance and zero mean.

and these data are subsequently ordinated using P.C.A., spurious results may be introduced owing to the effect of varying abundance scores arising from differential compaction during fossilization rather than any vegetational variables or depositional variables such as those giving rise to sorting.

Another problem with P.C.A. 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 controlling factors, and these are clearly critical when considering relations between the fossil assemblage and the living community. It becomes important to relate any structure or pattern within a stand ordination to those species characterizing the various parts of that structure, and the absence of any direct relation between stand and species ordinations arising from P.C.A. makes this process somewhat complicated.

CORRESPONDENCE ANALYSIS

Correspondence analysis (M. O. Hill, 1974), also known as *L'analyse factorielle des correspondances* (Escofier-Cordier, 1969; Benzecri, 1969, 1973), reciprocal averaging (M. O. Hill, 1973), and reciprocal ordering (Orloci, 1975), is an eigenvector method of ordination somewhat akin to P.C.A. ordination but one that overcomes some of the problems of P.C.A. Although it may be thought of as operating in a way similar to P.C.A., its rationale is developed from a different standpoint. The following is based on M. O. Hill (1973): A species (row) by stand (column) data matrix is constructed and an arbitrary set of species starting scores, between 0 and 100, is allocated. Preferably this should in practice reflect what is suspected as being the main gradient of change, as a good initial choice reduces the amount of calculation 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 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 that were fairly near the final scores of the first axis. These scores are then adjusted by subtracting a multiple of the first axis and the iterations continued until a new set of scores stabilize. These scores become

the second axis. The third and subsequent axes are derived in this way.

Strictly speaking, correspondence analysis should be used with contingency table data only, but continuous data can be analyzed by dividing the ranges of variates into a number of discrete pieces. If the pieces are small enough, an approximation to the continuous case is achieved (Naouri, 1970; M. O. Hill, 1974). David and others (1974) and Jöreskog and others (1976) suggest dividing the elements of the data matrix by the sum of all the elements in the matrix. The resulting proportions may be interpreted as probability values, and the matrix becomes a contingency table in the sense of Fisher (1940).

The simultaneous derivation of stand and species scores results in directly comparable ordinations. The species score is equal to the average 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 that 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 C.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." It should be stressed that the species scores derived by C.A. are corrected for species abundance, which, as pointed out, is not the case with unstandardized P.C.A., even though they may have the same distribution.

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

It should be noted that the eigenvalues quoted for the axes on the C.A. ordination are not measures of the variance extracted by the axes as given for the P.C.A. ordinations but rather a measure of the relation between the stand and the attribute ordinations (M. O. Hill, 1974). Orloci (1975) considers it "an indication of the conceptual difficulty with which the quadrats can be ordered based on the species scores."

CORRESPONDENCE ANALYSIS OF THE SILWOOD DELTA SURFACE-SEDIMENT DATA

The unconsolidated nature of the Silwood delta surface sediment facilitated the separation of whole leaves from fragments. Fragments and whole leaves were therefore separately treated in order to determine the contribution made by each to any paleoecological picture that might emerge.

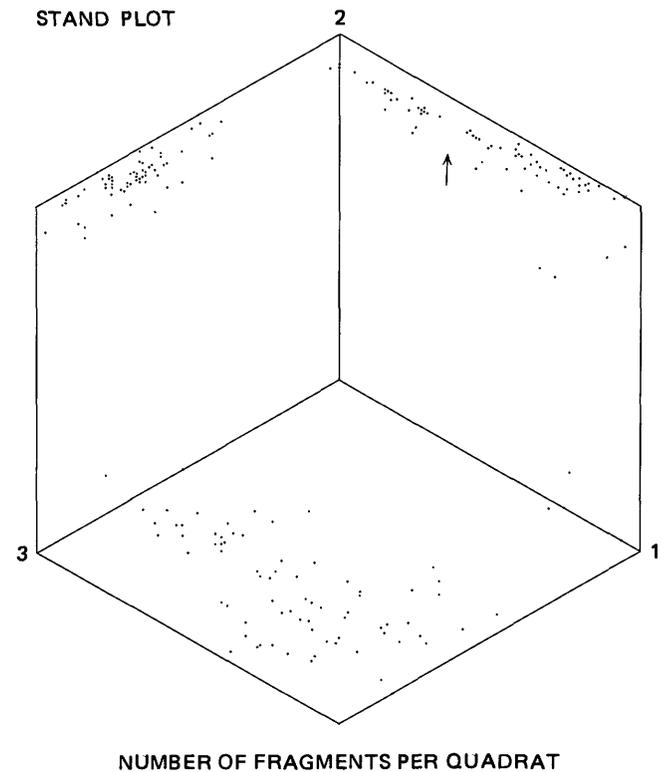
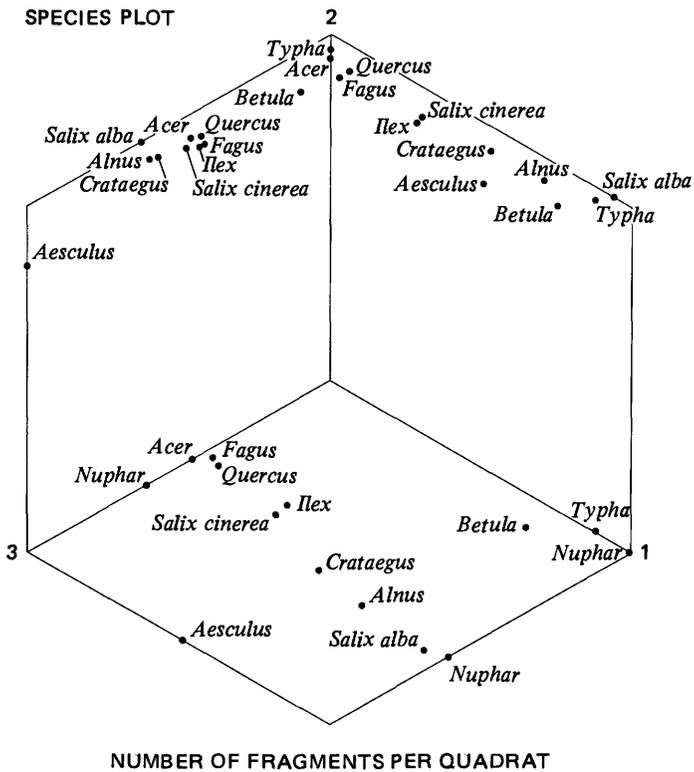
DENSITY MEASURES

The most straightforward estimate of leaf abundance is clearly a density measure, and this will be considered first. From the attribute (species) plot obtained by C.A. of the fragment density per quadrat of the twelve taxa determined from the delta deposits (fig. 53), it can be readily seen that the majority of species lies 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. Apparently *Nuphar* leaves have a very differ-

ent distribution pattern than other species. Such a result is perhaps to be expected because, being an obligate aquatic occurring only in the lake, the leaves of *Nuphar* are subject to dispersal processes different from leaves of 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. 54) shows a similar crowding of stands with high axis 2 scores, the only exceptions being those stands containing *Nuphar*.

It is apparent that the ordination of stands along axis 1 is not continuous: a minor break is indicated by an arrow. By examining the species plot (fig. 53), we find that the group of stands to the left of the arrow in figure 54 (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*. In contrast, the group to the right of



ESTIMATE OF EIGENVALUE

- Axis 1 (E1) = 0.25
- Axis 2 (E2) = 0.09
- Axis 3 (E3) = 0.07

FIGURE 53.—Correspondence analysis ordination of fragment densities per quadrat as sampled from the delta surface sediment of Silwood Lake. Twelve species ordinated. View depicts three internal faces of a cube onto which the positions of the species in three-dimensional space have been projected. Thus there are three times as many points in total plot as there are, in this case, species. Numbers 1, 2, and 3 at corners of plot denote three axes originating from center of diagram.

FIGURE 54.—Stand plot from same ordination as in figure 53. Arrow marks discontinuity in ordination along axis 1.

the arrow (that is, 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 (data table 1), it is apparent that this is so. (*Typha* in this case probably includes a small number of fragments of other monocotyledonous plants, for example, grasses.)

Not all of the 12 species ordinated here occur as whole leaves. In order to compare legitimately 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. 55 and 56) 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. This dissimilarity of the *Betula* distribution was previously depicted on axis 3 of figure 53 along with that of *Typha*. It therefore follows that those species accounting for the greatest variation within the "Alnus group" of figure 54 are dominantly *Nuphar*, then *Betula* and *Typha*. The separation of *Aesculus* on axis 3 of

figure 55 suggests that further variation is accounted for by the distribution of this species.

The discontinuity in the ordination on axis 1 of figure 56 is still 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. Figure 57 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 percent of the streamflow (fig. 48). Distributary 3, however, passed through the *Typha* bed before crossing the exposed delta surface; 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.

The pattern of leaf-fragment distribution on the delta surface evidently is primarily controlled by the pattern and energies of the distributaries. It was ear-

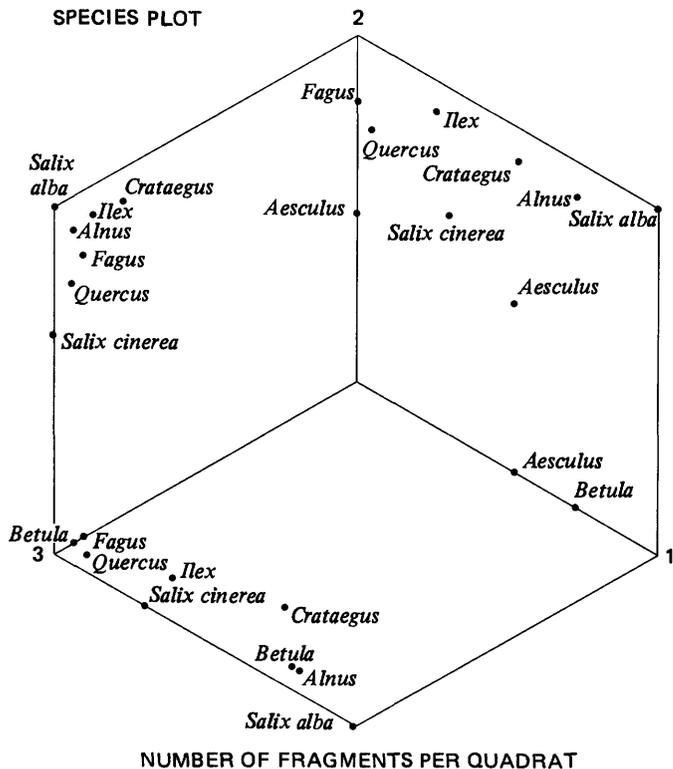


FIGURE 55.—Fragment-density plot from Silwood delta surface sediment. *Nuphar*, *Typha*, and *Acer* densities were not included in ordination (see text).

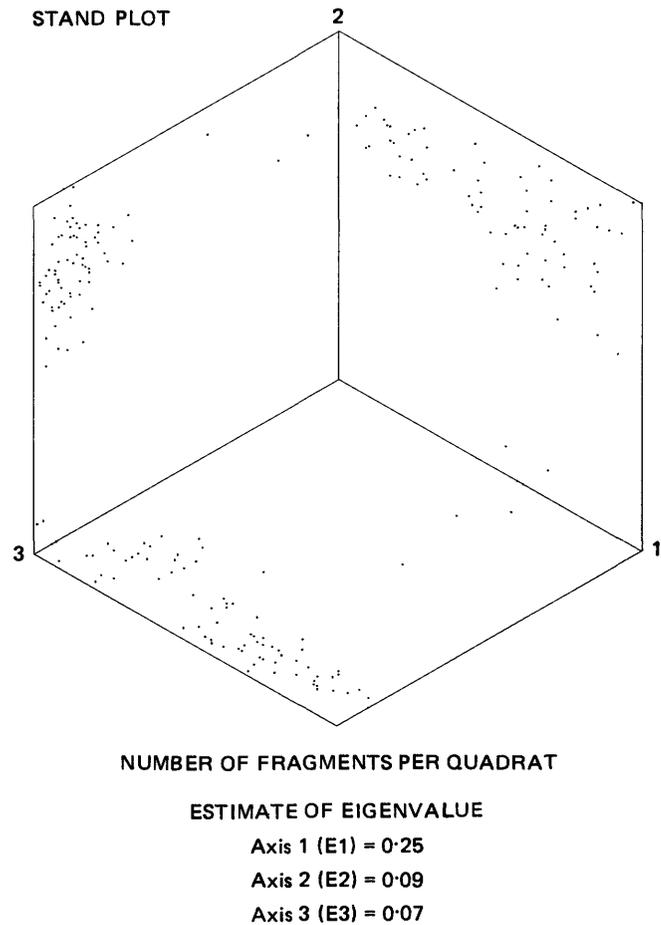


FIGURE 56.—Stand plot of fragment density based on data not including densities of *Nuphar*, *Typha*, and *Acer*.

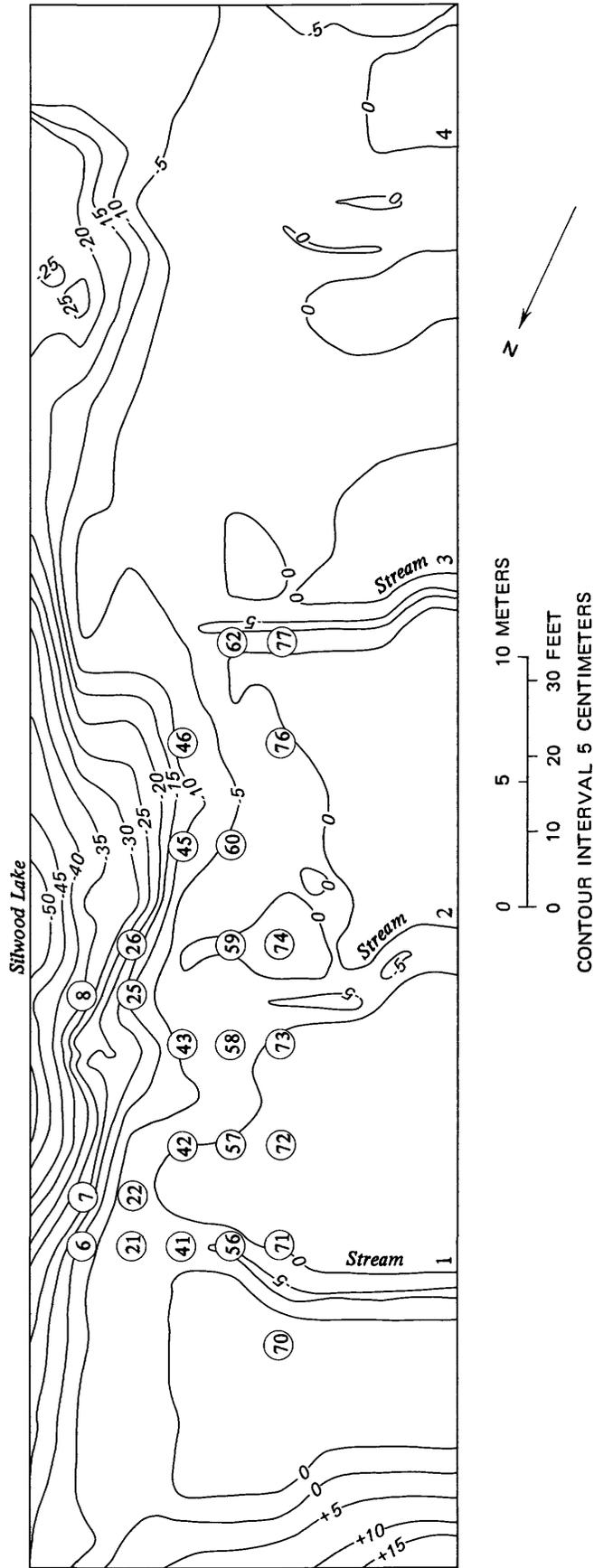


FIGURE 57.—Position of those stands (quadrats) constituting *Fagus/Quercus* group of figures 54 and 56 with respect to delta contours. Ordination carried out using leaf fragment density data.

lier pointed out that most leaf fragmentation was by biological and mechanical degradation during water transport; it is not surprising, then, 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 figures 54 and 56 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, constituting the "*Alnus* group," represents the more local flora.

From the arguments presented in the section entitled "Leaf Degradation," 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. The most striking feature about the C.A. ordination plot of the whole-leaf densities in the quadrats from the Silwood delta, figure 58, is the separation, on axis 1, of *Fagus*, which suggests a marked difference in distribution from the other species. The stand plot, figure 59, shows no obvious discontinuities in the data, but there is possibly a gap halfway along axis 1. If stands with an axis 1 score of less than 50 are plotted back onto 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, apparently are not related, as *Fagus* and *Quercus* plot apart in figure 58.

The delta water-trap data (table 2) indicate that approximately twice the number of *Quercus* leaves land directly on the delta surface by wind transport as *Fagus* leaves. On the other hand, the results of the leaf-degradation experiments (figs. 27-43) indicate 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 (data table 2).

On axis 1 in figure 58, *Quercus* plots close to the local

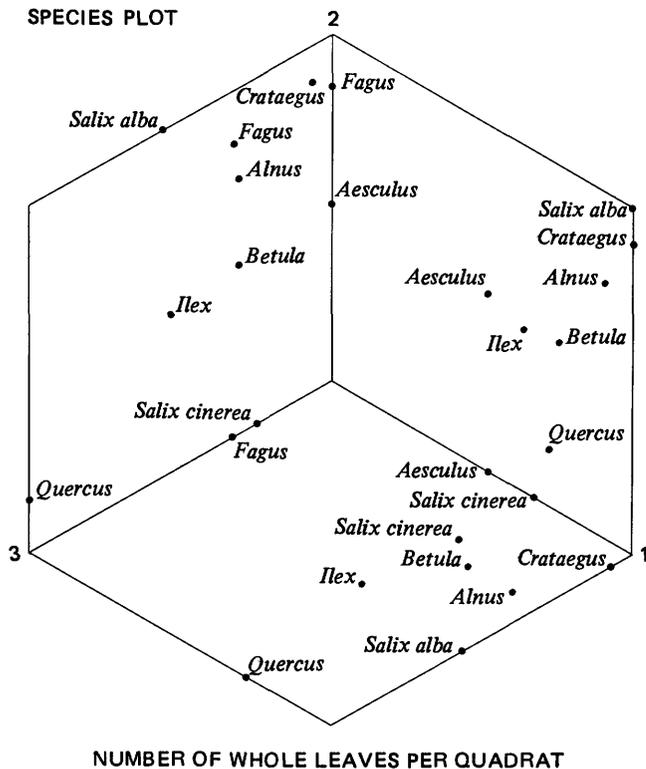


FIGURE 58.—Correspondence analysis species ordination plot based on whole-leaf density data from surface sediment of Silwood delta.

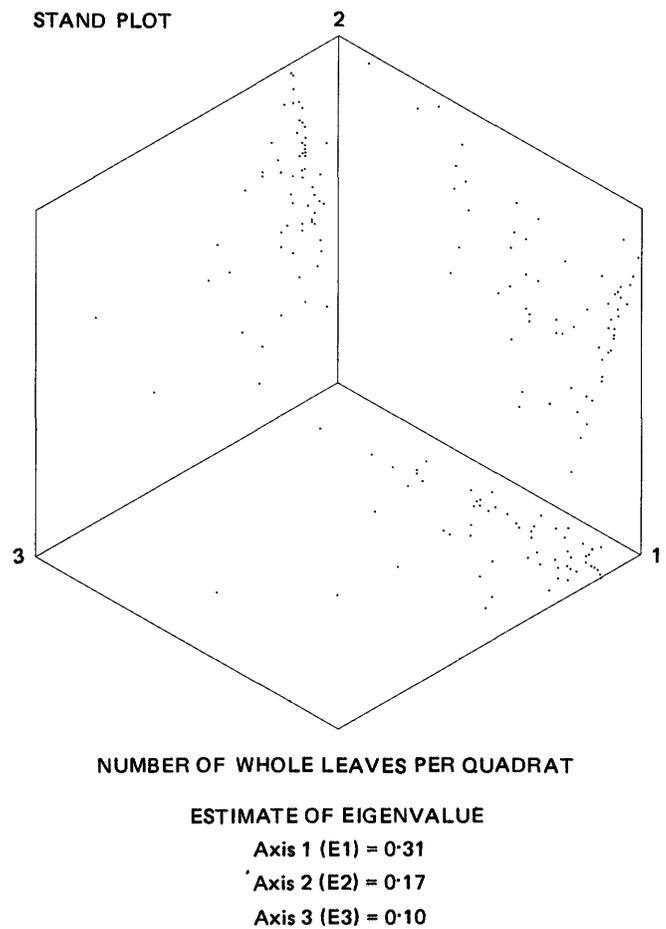


FIGURE 59.—Companion stand plot to figure 58.

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 be regarded as local. The only way that leaves of these trees can enter the lake deposits is by direct wind transport, hence the *Quercus* plotting, along with *Alnus* and others, on axis 1 of the whole-leaf density ordination (fig. 58). Axis 2, however, separates *Quercus* and *Salix cinerea* from the other species, suggesting that they differ in distribution. In the case of *Quercus*, the difference 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 discussion. Although clearly a local species, the contribution of leaves directly to the delta by wind transport is small (data table 2), probably because *S. cinerea* rarely attains a height greater than 3 m on the delta and the *Typha* bed effectively traps any airborne leaves before they reach the lake. Observations made during sampling indicate that this was so because the leaf litter trapped on the *Typha* bed was rich in *Salix* leaves. Most of the leaves must therefore enter the deposit by the stream, and, as a result, *S. cinerea* consistently plots near *Quercus*, which exhibits a "mixed" origin.

It is possible 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 a more distant element rich in *Fagus*. *Quercus* appears to be a component of both local and distant floras, as apparently is *Salix cinerea*. The positions of *Ilex*, *Aesculus*, and *Crataegus* appear to be intermediate.

The special position of *Nuphar* may at first present some problems, but anatomical studies would soon reveal the likelihood of its being an aquatic plant. Some measure of paleocommunity 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 if it is assumed that most 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. It is pointless to calculate the percentage cover, since all the quadrat volumes are the same.

On a plot of the total fragment areas per quadrat of all the leaves of the 12 taxa found in the Silwood data sediments, figure 60, axis 1 clearly separates out *Nuphar* from the other species. Reference to the raw data (data table 3) suggests a possible reason. In addition

to the difference in distribution, the morphology of the large *Nuphar* pads is totally different from that of any of the other species: consequently, their fragments can exhibit a much greater size range than any other species. The total area of *Nuphar* can be seen to fluctuate greatly from quadrat to quadrat. The data concerning *Aesculus*, which has comparatively large leaflets, also show this pattern, again reflected in the ordination of figure 60, because *Aesculus* is separated from the other species on both axes 2 and 3.

The stand plot (fig. 61) 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 figure 60. The position of these stands on the delta surface is shown in figure 62. Clearly the pattern derived from the density measures (figs. 53 and 54) is being repeated, which suggests that the cover abundance measures, despite the powerful morphological effect, are retaining sedimentary-pattern information.

The ordination would not be so easily interpreted if one of the species determining the lower group was morphologically very different from the others. This effect can be seen to some extent in figures 63 and 64. Here the species not occurring as whole leaves (*Nuphar*, *Typha*, and *Acer*) have been excluded. The

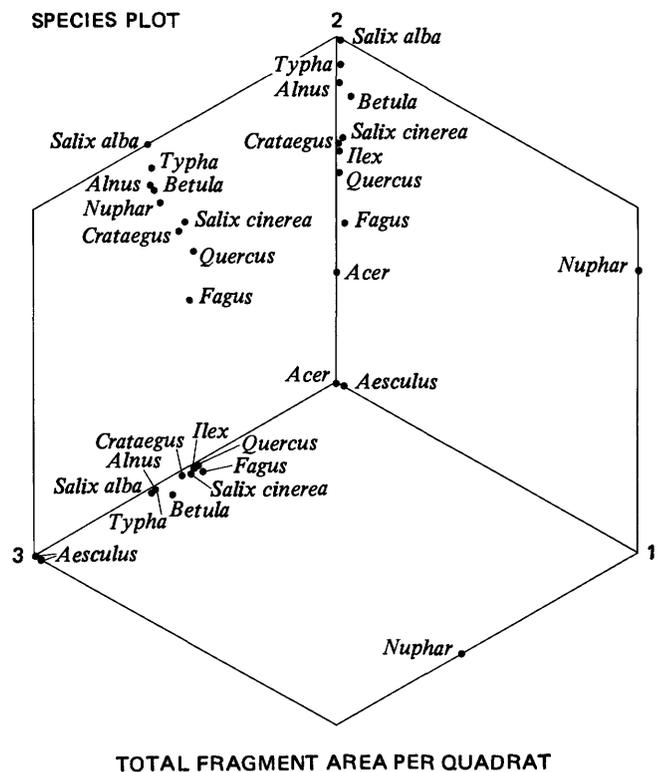


FIGURE 60.—Correspondence analysis ordination of leaf fragments from Silwood delta surface sediment based on "cover" rather than density.

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 toward the separation of the *Fagus/Quercus* group on axis 2 of figure 61, the separation of the stands into two groups is not so well defined. Those stands occurring to the left of the apparent discontinuity (arrow) on axis 1 (fig. 64) are in fact, the same as those plotted in figure 62.

When the species are ordinated on the basis of the whole-leaf total area per quadrat (data table 4; fig. 65), *Fagus* is separated from the other species on axis 1 as in ordinating the whole-leaf density data (fig. 58). *Aesculus* is further separated from the main group, and its difference picked out strongly on axis 3. Once again, this may be interpreted as primarily a morphological effect. Except for this difference, 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. 66) exhibits the same pattern on axes 1 and 2 as in figure

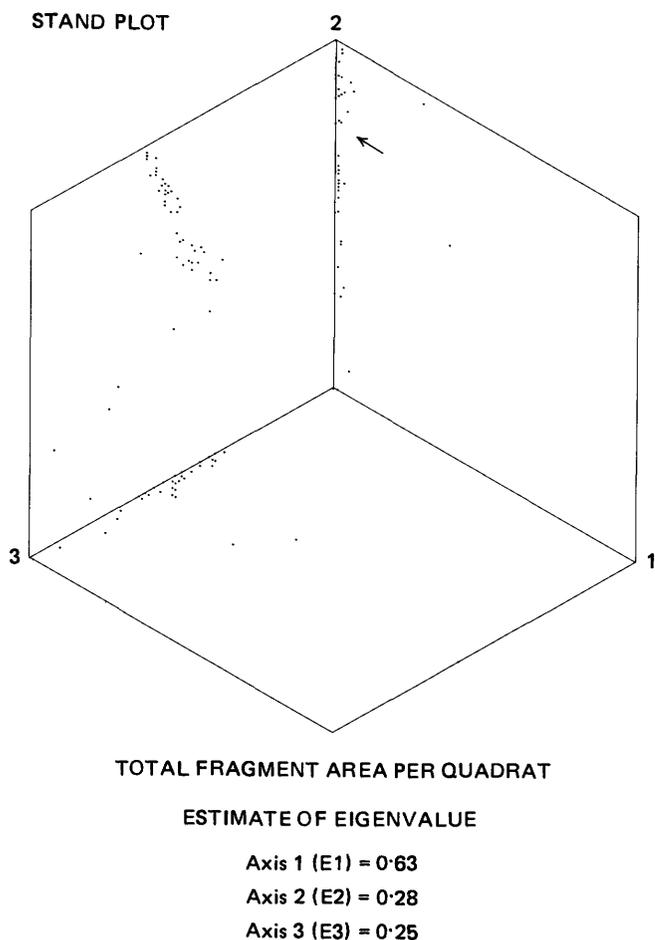


FIGURE 61.—Correspondence analysis ordination of fragment areas per quadrat. Apparent discontinuity in stand ordination on axis 2 marked by arrow. Points below arrow represent those stands relatively rich in *Fagus* and associated species.

59. The variation on axis 3, however, now separates those stands rich in *Aesculus* rather than *Quercus*. The separation of *Quercus* from the "local" group as a result of 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 (data table 5), the resultant ordination has the appearance of figures 67 and 68. This type of data approximates a cover abundance measure for each species.

The magnitude of the data scores for species that are local to the site and those with leaves resistant to degradation will tend to be largely determined by the number of size of the whole leaves. For other species, fragment size and number will be critical. Clearly those taxa producing large leaves will amass large cover scores even if only a few individuals are present in each quadrat. As expected, 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* is separated on axis 1. The cause for this is probably not so much its morphology as its resistance to degradation. As indicated in table 3, *Fagus* fragments constitute only some 26 percent of the total area of *Fagus* occurring in the sampled delta deposits. Where *Fagus* occurs, then, the cover will commonly 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 scores. 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, any pattern caused by sedimentary processes is lost. The prospects of detecting such patterns are much better if density measures are used, because, with increased degradation, the fragment density in the distributaries increases and better contrast between the stream distributaries and the rest of the delta surface is obtained.

CONCLUSIONS

The large number of simultaneously operating processes that result in the formation of an allochthonous plant fossil deposit require that any study of the sorting and deposition of plant material be of a multidisciplinary nature. A restricted study of the kind described here cannot be definitive, but certain conclusions can be drawn, some of which may seem obvious on reflection, others not so. Much has been taken for granted in

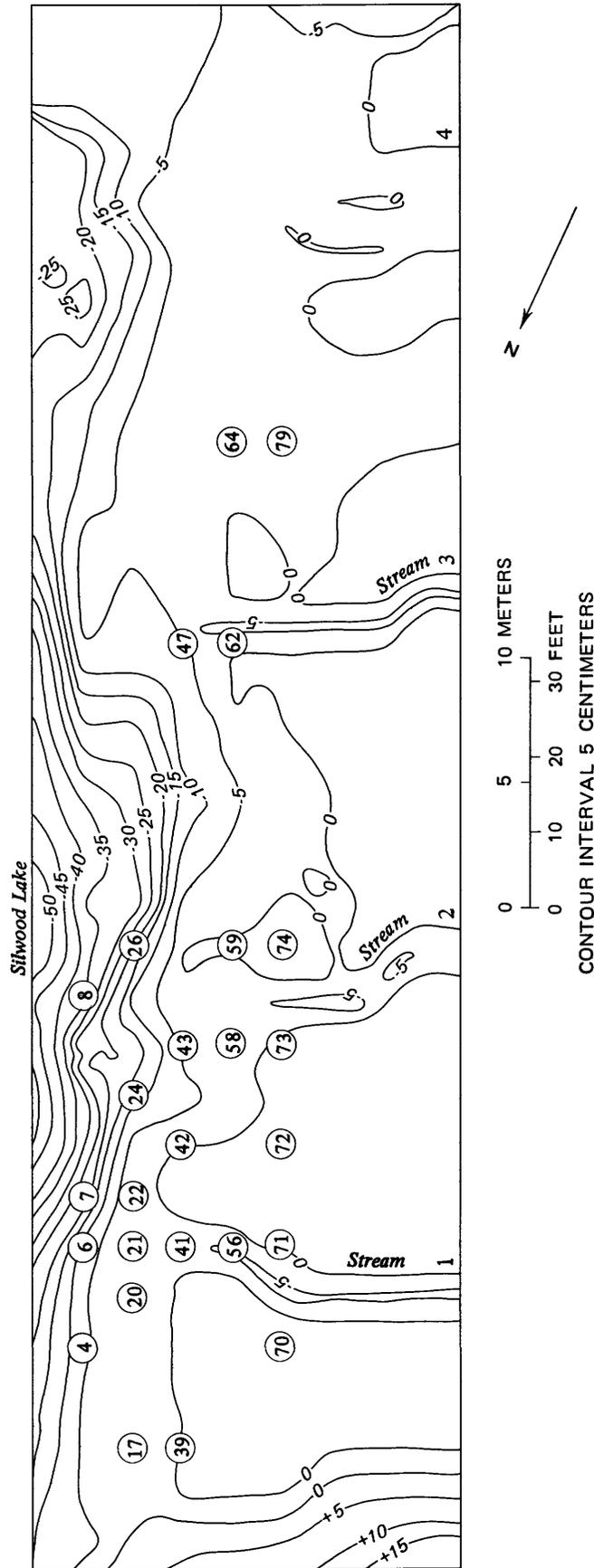


FIGURE 62.—Positions of those stands (quadrats) constituting lower group on axis 2 of figure 61. This group, again rich in *Fagus* and *Quercus*, is the result of an ordination based on cover data.

the past concerning the mechanisms of sorting and deposition, but if paleobotany is ever to gain from a more quantitative approach, then even the most basic assumptions must be tested.

From the results of the present study and a consideration of the number of variables involved, it is not likely that any direct relation will ever be found to link the abundances of the source vegetation component species and their representation in an allochthonous fossil assemblage. The factors affecting litter production alone are sufficiently numerous to introduce significant 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 (for example, percent scales) also means that overrepresentation of riparian plants seriously biases the proportions of the other taxa. Even species that are clearly local to the depositional environment will be seriously underrepresented where growing behind a screen of other vegetation.

Although proportional representation of the source taxa is not to be expected, information relating to rela-

tive positions of the source species with respect to the depositional site might be preserved in the fossil assemblage.

A theoretical approach to the study of fluid transport and deposition of plant material is hampered by parameters of the plant material itself. The two-dimensional nature of most plant debris, progressive waterlogging, colonization by microorganisms, and fragmentation during transport make impossible the use of fluid dynamics equations for predicting transport and deposition phenomena. An empirical approach was therefore adopted for this study.

Experiments with both artificial and natural leaves showed that weight per unit area is the single most critical factor affecting the transportability of a leaf by wind. Yet only the small dense sun leaves growing at the top of a tree crown are exposed to wind energies sufficient to insure a chance of long-distance transport. This factor alone results in significant biases in the leaf-size distribution within a laterally extensive lacustrine fossil-plant assemblage. In fossil-leaf as-

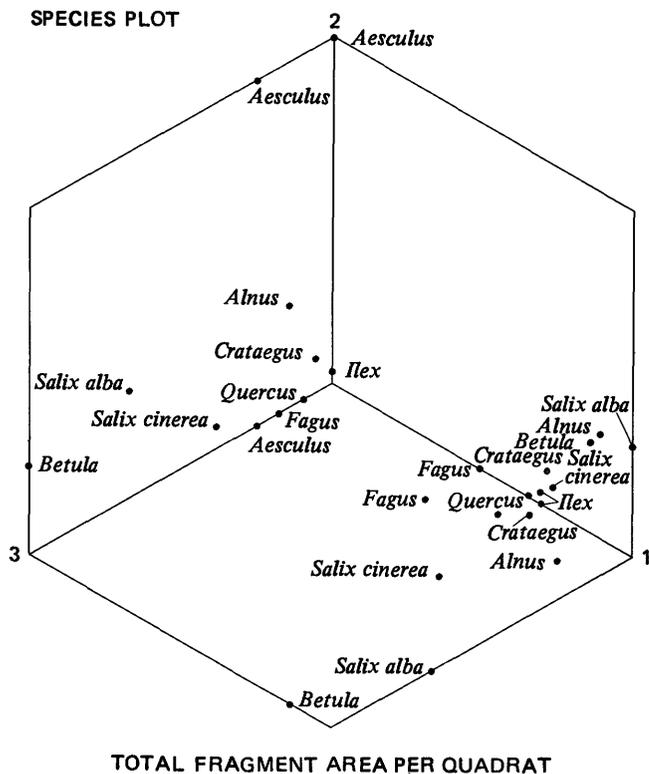


FIGURE 63.—Correspondence analysis ordination based on "cover" abundance of nine taxa: *Fagus*, *Quercus*, *Alnus*, *Betula*, *Salix cinerea*, *Ilex*, *Aesculus*, *Salix alba*, and *Crataegus*.

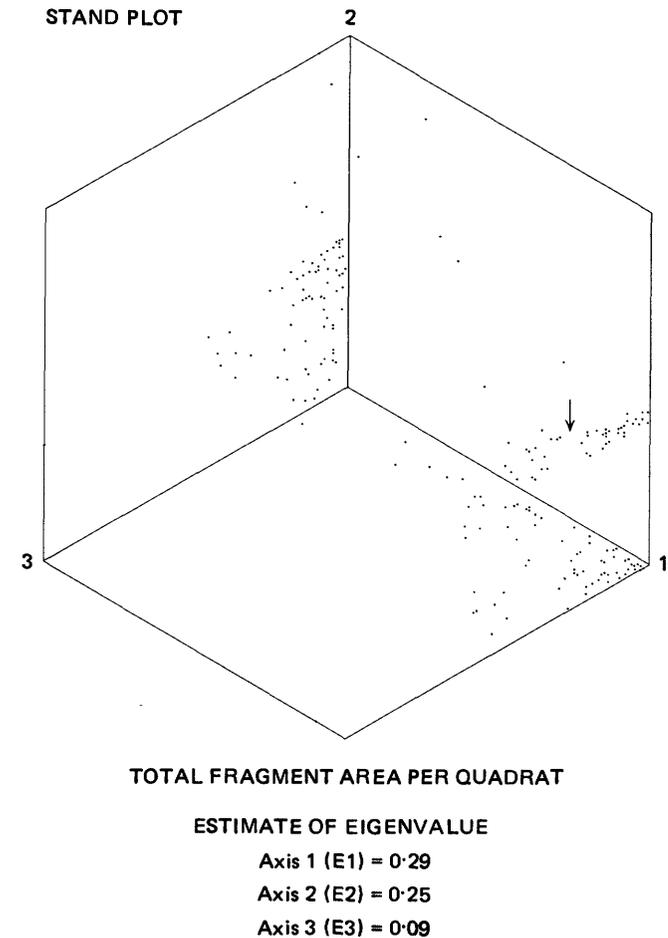


FIGURE 64.—Stand ordination based on "cover" abundance and a companion plot to figure 63. Arrow marks apparent discontinuity of ordination on axis 1.

semblages deposited in an open-lake environment, a large part of the source vegetation will be represented only by small sun leaves, and paleoclimate interpretation based on such an assemblage could be wrong. Swamp and small lake basins, where the lake width is minimal relative to the forest canopy height, are likelier to contain leaf assemblages that accurately reflect the leaf-size populations within the source vegetation, because both sun and shade leaves will be represented throughout the deposit.

Unlike wind transport, aqueous transport usually involves extensive degradation of the plant material. Fragmentation may be categorized according to the casual agency, mechanical or biological. Biological degradation, which can take place in both stream and lake bottom environment, may be divided into that produced by invertebrate detritivores, both large-particle feeders and small-particle feeders, and that brought about by microorganisms.

Fresh material is comparatively robust, but microbial colonization predisposes leaves to invertebrate attack and mechanical fragmentation within a few weeks of entering an aqueous environment. Chemical rather than morphological leaf characteristics affect the rate of microbial breakdown, which in turn affects subsequent degradation.

Because mechanical fragmentation occurs predominantly as a result of water transport, examination of

the fragmentary condition of a fossil can be paleoecologically useful. By examining the type of degradation, particularly in a fluviolacustrine environment, it should be possible, even in the absence of inorganic sedimentary structures, to distinguish those leaves transported from upstream from those that grew locally. Leaves representing upstream plants will exhibit the rounded holes indicative of invertebrate attack, the loss of intercostal tissue produced by microorganisms, and the angular breaks brought about by mechanical damage. The local leaves deposited in the lake will lack extensive mechanical fragmentation.

From the cores taken throughout the Silwood delta, it is evident that two physically distinct leaf beds were formed, one related to the lake-bottom deposits and one at the top of the stream-derived deltaic sediments. Their separation is the result of the leaves and sediment with different hydrodynamic properties being acted upon by the fluid stresses at the stream/lake interface.

At Silwood, no obvious differences in species composition were noted between the upper leaf bed (1) and

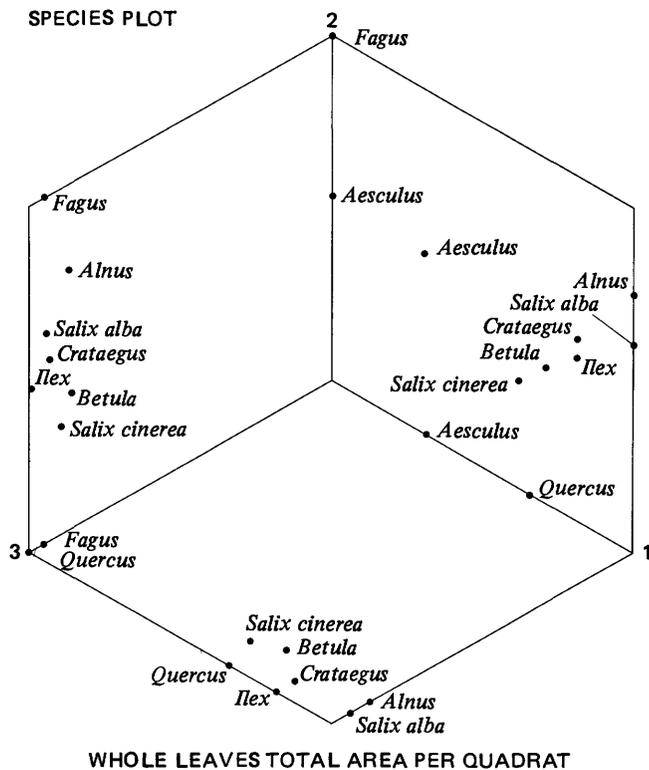


FIGURE 65.—Species plot of whole-leaf "cover" data.

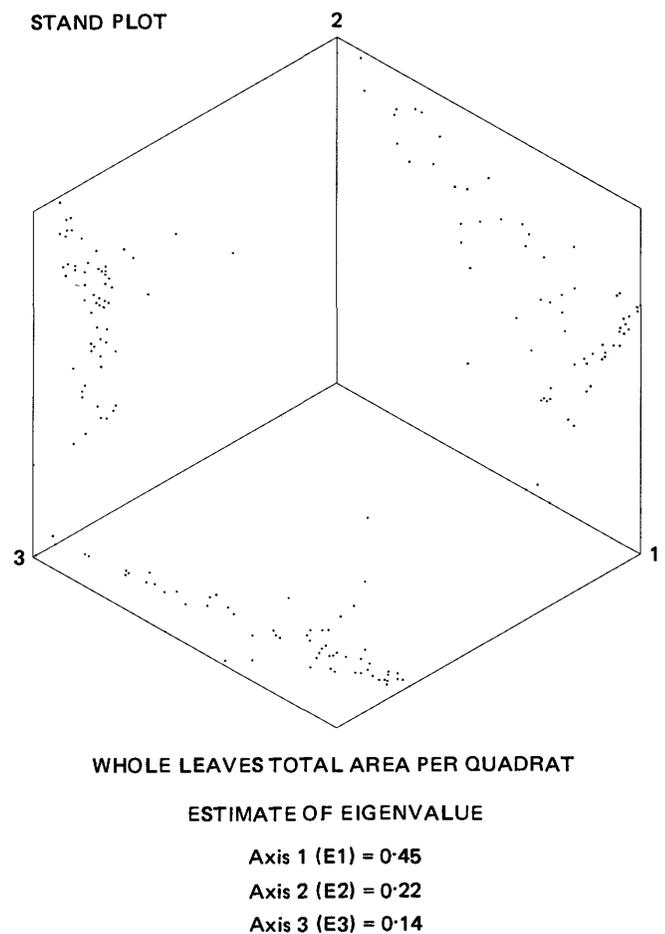


FIGURE 66.—Companion stand plot to figure 65.

the lower leaf bed (2); this is attributed to the rapid biological destruction of *Alnus glutinosa* leaves on the lake bottom. Only the more resistant *Quercus* and *Fagus* leaves survived to be incorporated in the lower leaf bed, thereby making the species composition of the two leaf beds appear similar.

On the evidence available, generalizations cannot be made concerning the susceptibility of riparian plants to biological destruction. If, under different circumstances, the leaves from trees bordering the lake were resistant to breakdown, a considerable difference in species composition between the upper and lower leaf beds would exist to reflect the relative growth positions of the source taxa. Leaf bed 1 may represent those species growing some distance upstream from the depositional environment admixed with leaves from the local streamside plants, leaf bed 2 the local lakeside vegetation.

The physical separation of the beds is dependent upon the relative settling velocities of the leaves and sediment. In the Silwood environment, where the leaf material had a settling velocity greatly exceeding that of the sediment, the bulk of the plant debris that was transported as bedload collectively settled out at the top of the foreset slope. In higher energy environments, where the inorganic sediment settling velocity would

approach or exceed that of the plant debris, the separation of the leaf beds might be lost.

If two physically different leaf beds separated by fine-grained sediment devoid of any concentration of plant material are identified in a fossil deposit and can be related to the type of deposition described here, the patterns of deposition of the plant fossils could be used to reconstruct the source vegetation in some detail. The upper deltaic leaf bed will contain mechanically fragmented plant remains from vegetation growing upstream and may represent slope plants as well as those growing on consolidated deltaic deposits. The lower leaf bed will contain fossils representing the local lakeside vegetation together with some leaves blown in by long-distance wind transport and some stream-transported leaves that were still floating on arrival at the lake. Evidence of mechanical degradation will be minimal.

As infilling of the lake basin progresses, the species composition of the upper leaf bed is likely to change as leaves from distantly growing species are filtered out by the developing delta vegetation and leaf input from

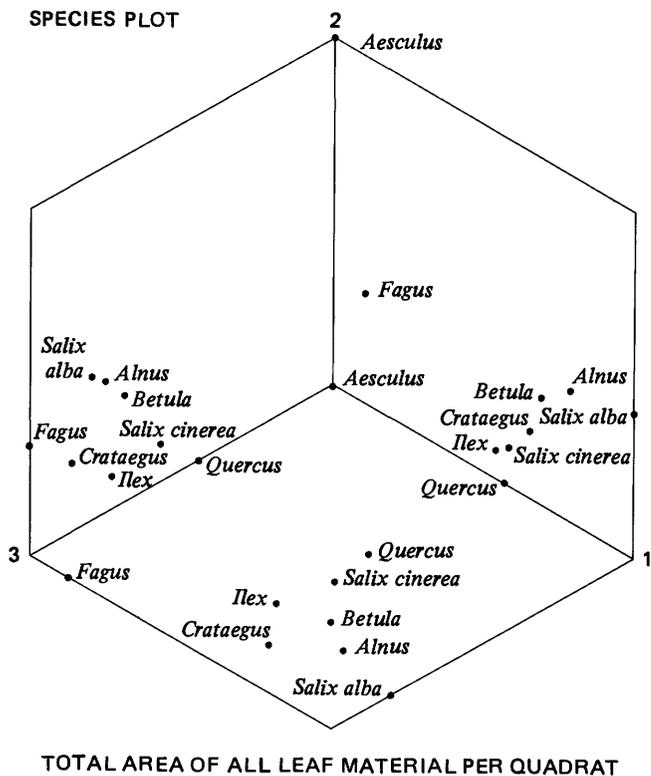


FIGURE 67.—Correspondence analysis ordination of combined whole-leaf and fragment "cover" abundance data.

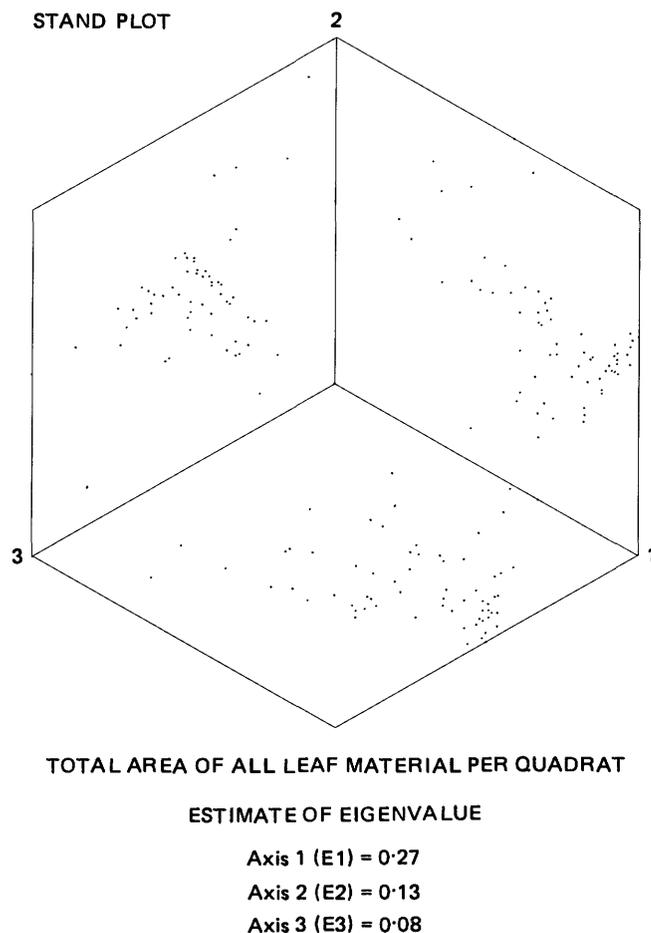


FIGURE 68.—Companion stand plot to figure 67.

the delta vegetation increases. A lateral change in species composition, then, may reflect a short-term temporal change in species distribution, whereas a difference in species composition between the upper and lower leaf beds (assuming no disproportionate degradation of leaves from one component of the vegetation has taken place) at any point might reflect a spatial separation of taxa within the source vegetation.

Any heterogeneity in species distributions that might originally be present within a body of sediment at the time of deposition could be seriously distorted by postdepositional differential degradation. In the Silwood deposit, we find an almost complete loss of the locally abundant *Alnus glutinosa* leaves from the lake bottom. It is only when deposition is abnormally rapid that such species are preserved. Because preservation is evidently linked to speed of burial, analysis of fossil remains should include specimens from all parts of a deposit, not just those occurring within concentrated leaf beds, and evidence of rapid burial should not be ignored. Detailed analysis of those plant remains that are consistently found only in association with coarse or poorly sorted sediments may provide critical clues as to the nature of those parts of the flora normally missing from the fossil record owing to a lack of resistance to biological degradation. For this reason, highly fragmented remains as well as well-preserved "museum" specimens should be collected, for it is the fragmented material that is likely to contain more paleoecologically useful information. Species abundance and type will commonly vary as a function of lithologic type even though all remains represent the same vegetation.

When quantitatively sampling fossil plant deposits, a large number of factors, primarily lithologic, prevent the sampling regime's being ideal; consequently, robust statistical methods have to be used to analyze the resulting data. The usefulness and ability of both principal components analysis (P.C.A.) and correspondence analysis (C.A.) to detect and display trends and sometimes discontinuities within the data is self evident; on both theoretical and practical grounds, C.A. is more suitable for the analysis of paleobotanical data. The duality of the stand and species plots make C.A. particularly useful for detecting the relations between assemblage structure and lithology, and C.A. ordinations are not affected by overall species abundance. There can be no doubt that future investigations will confirm a correspondence analysis as a powerful paleoecological tool.

Work described here represents an investigation of only a single depositional environment; consequently, any extrapolation of the findings to situations other than a fluvial lacustrine delta system must be done with

care. Nevertheless, attempts have been made to generalize whenever possible, and by studying a number of aspects of what, after all, is a multivariate system, it has been possible to assess the relative importance of some factors that determine structure in a plant-fossil deposit.

The following generalizations can be made regarding the investigation of a fossil-plant deposit with a view to reconstructing the positions of various source taxa relative to the depositional site:

- (1) Detailed study is required not only of the fossil material but also of the lithology and sedimentary structure of the entombing matrix.
- (2) The sediments above and below the fossil material should be studied to ascertain relative deposition rates (and thereby the likelihood of preservation of species normally susceptible to rapid degradation) and, if possible, basin geometry.
- (3) Sampling should be carried out in an objective manner and include comparatively unfossiliferous sediments.
- (4) Fragmentary as well as complete specimens should be collected.
- (5) The type, biological or mechanical, and degree of fragmentation should be determined within each sample.
- (6) Where possible, sampling should be carried out with the aim of determining the three-dimensional nature of the fossil deposit.
- (7) Individual samples should not cross boundaries of sedimentary units.

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DATA TABLES 1–5

Silwood delta fragment density and whole-leaf density and area data
 [Material collected from top 2 cm of delta sediment]

DATA TABLE 1.—*Silwood delta fragment density per quadrat*

Stand	<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Salix cinerea</i>	<i>Ilex</i>	<i>Aesculus</i>	<i>Acer</i>	<i>Crataegus</i>	<i>Typha</i>	<i>Nuphar</i>	<i>Salix, Alba</i>
1	1	7	0	0	4	0	0	0	0	0	7	0
2	5	3	0	1	0	2	0	0	0	0	0	0
3	6	0	1	0	1	0	0	0	0	0	0	0
4	9	4	1	3	3	0	4	0	0	0	0	0
5	14	2	1	1	6	2	0	0	1	1	0	0
6	18	4	7	15	0	8	0	1	0	1	0	0
7	17	0	10	21	12	3	2	1	0	1	0	0
8	29	5	16	30	16	10	2	1	1	9	0	0
9	23	2	3	5	2	1	0	0	0	14	0	0
10	94	21	0	2	17	5	2	0	1	19	0	5
11	55	7	0	4	24	3	0	0	0	5	0	0
12	0	11	0	3	5	0	0	0	0	8	0	0
13	89	6	2	7	14	3	0	0	0	10	0	4
14	43	4	0	1	4	1	0	1	0	6	0	2
15	48	2	0	4	4	1	0	0	0	3	0	0
16	22	8	0	4	1	0	0	0	0	2	0	2
17	12	2	4	0	3	0	3	0	0	1	3	0
18	3	0	0	0	0	0	0	0	0	0	1	0
19	4	2	0	0	1	0	0	0	0	0	0	0
20	9	0	0	2	0	2	1	0	0	1	2	0
21	7	0	7	10	9	2	0	0	0	1	1	0
22	11	1	7	8	6	7	1	0	1	0	1	0
23	24	0	6	8	4	2	0	0	0	0	2	0
24	5	2	2	0	2	3	0	0	0	0	7	0
25	29	2	8	22	7	15	0	0	0	3	0	0
26	5	1	9	0	5	6	0	0	0	2	0	0
27	90	18	3	20	38	4	1	0	0	12	0	2
28	6	0	0	0	1	0	0	0	0	2	0	0
29	10	2	1	2	5	0	0	0	0	0	0	0
30	13	0	1	2	2	1	0	0	0	2	0	0
31	23	7	0	1	4	0	0	0	0	5	0	0
32	22	7	2	2	3	1	0	0	0	1	0	0
33	28	5	2	2	10	2	0	0	0	6	1	1
34	16	0	0	0	0	0	0	0	0	3	0	1
35	10	2	0	1	2	2	0	0	0	2	0	0
36	11	8	0	2	1	3	0	0	0	4	0	0
37	8	2	0	1	0	0	0	0	0	2	1	0
38	5	1	0	1	1	0	0	0	0	3	0	0
39	8	1	1	1	1	0	2	0	0	0	0	0
40	3	0	0	1	0	0	0	0	0	0	0	0
41	31	10	38	59	55	8	1	1	0	0	0	0
42	28	5	8	16	6	6	0	0	0	7	0	0
43	13	2	7	17	3	6	0	0	0	0	0	0
44	6	4	5	8	5	4	1	0	0	1	0	1
45	7	3	0	2	2	0	0	0	0	1	0	1
46	8	1	6	4	1	3	0	0	0	1	0	0
47	30	5	18	1	5	2	0	0	0	3	0	0
48	8	2	0	4	6	1	0	0	0	1	0	0
49	22	1	1	5	4	3	0	0	0	2	0	0
50	12	4	1	3	1	0	0	0	0	0	0	0
51	11	5	2	3	1	4	0	0	0	2	1	0
52	0	4	0	1	1	0	0	0	0	2	0	0
53	20	2	0	0	0	1	0	0	0	6	0	0
54	11	6	0	0	1	0	0	0	0	5	1	0
55	6	2	0	2	2	0	0	0	0	0	0	0
56	36	0	54	100	58	5	0	1	0	0	0	2
57	3	1	3	3	1	3	0	0	0	0	0	0
58	15	5	6	17	2	0	1	0	0	0	0	0
59	0	5	13	16	6	3	0	0	0	6	2	0
60	3	0	2	3	3	0	0	0	0	1	0	0
61	11	3	2	6	3	3	1	0	0	2	0	0
62	8	3	3	2	3	0	0	0	0	0	0	0
63	9	1	1	0	0	0	0	0	0	0	0	0
64	5	0	4	6	2	1	0	0	0	0	0	0
65	12	6	1	5	7	0	0	0	0	0	0	0
66	15	0	0	7	7	1	0	0	0	0	1	0
67	24	5	0	2	8	0	0	0	0	0	0	0
68	2	0	0	0	1	0	0	0	0	0	0	0
69	10	5	3	1	3	1	0	0	0	7	0	0
70	4	1	3	5	3	2	0	0	0	3	0	0
71	11	0	8	7	26	7	0	0	0	1	0	0
72	2	1	1	3	1	2	0	1	0	0	0	0
73	4	0	3	10	9	1	0	0	0	0	0	0
74	14	5	6	14	5	4	0	0	0	0	0	0
75	6	2	2	3	1	2	0	0	0	0	0	0
76	39	11	16	13	12	2	1	0	0	1	0	0
77	4	3	5	6	2	1	0	0	0	4	0	0
78	5	4	1	2	4	0	0	9	0	0	0	0
79	7	3	3	12	6	0	0	1	0	0	0	0

DATA TABLE 2.—*Silwood delta whole-leaf density per quadrat*

Stand	<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Salix cinerea</i>	<i>Ilex</i>	<i>Aesculus</i>	<i>Acer</i>	<i>Crataegus</i>	<i>Typha</i>	<i>Nuphar</i>	<i>Salix, Alba</i>
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	1	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	1	0	0	0
6	11	1	2	1	5	0	0	0	0	0	0	0
7	11	1	0	0	4	0	1	0	0	0	0	0
8	23	10	9	1	26	0	1	0	0	0	0	0
9	27	0	0	2	6	0	0	0	0	0	0	0
10	87	19	1	4	24	0	0	0	1	0	0	0
11	27	2	0	3	15	0	0	0	0	0	0	0
12	18	4	1	3	11	0	0	0	0	0	0	0
13	57	15	0	1	18	1	0	0	0	0	0	0
14	37	3	1	3	4	1	0	0	0	0	0	0
15	55	12	0	7	6	0	0	0	0	0	0	0
16	47	7	0	0	3	0	0	0	1	0	0	0
17	16	2	10	1	12	0	2	0	0	0	0	0
18	3	1	6	0	0	1	0	0	0	0	0	1
19	4	0	3	0	1	0	0	0	0	0	0	0
20	1	1	16	0	0	0	0	0	0	0	0	0
21	1	1	0	4	0	0	0	0	0	0	0	0
22	1	0	1	1	1	0	0	0	0	0	0	0
23	2	0	4	0	1	0	0	0	0	0	0	0
24	2	1	0	0	1	0	0	0	0	0	0	0
25	12	4	3	2	23	1	0	0	0	0	0	0
26	6	2	2	0	6	0	0	0	1	0	0	0
27	46	5	0	6	40	0	0	0	0	0	0	0
28	1	0	0	0	2	0	0	0	0	0	0	0
29	2	1	0	1	1	0	0	0	0	0	0	0
30	1	1	0	1	3	1	0	0	0	0	0	0
31	5	2	0	2	11	0	0	0	0	0	0	0
32	11	1	0	0	2	0	0	0	0	0	0	0
33	16	2	0	1	8	0	0	0	0	0	0	0
34	16	1	1	0	0	0	0	0	0	0	0	0
35	10	2	0	0	1	0	0	0	0	0	0	0
36	3	1	0	0	2	0	0	0	0	0	0	0
37	8	4	0	0	1	0	0	0	0	0	0	0
38	12	1	0	0	8	0	0	0	0	0	0	0
39	3	0	7	2	2	0	0	0	0	0	0	0
40	0	0	1	0	0	0	0	0	0	0	0	0
41	7	2	5	2	27	0	0	0	0	0	0	0
42	0	0	0	0	3	0	0	0	0	0	0	0
43	0	0	1	0	1	0	0	0	0	0	0	0
44	0	1	0	1	4	0	0	0	0	0	0	0
45	14	4	9	2	1	0	0	0	0	0	0	0
46	1	0	2	0	0	0	0	0	0	0	0	0
47	1	3	3	0	3	0	0	0	0	0	0	0
48	1	3	0	0	3	0	0	0	0	0	0	0
49	1	1	0	0	4	0	0	0	0	0	0	0
50	2	1	0	0	1	0	0	0	0	0	0	0
51	3	0	1	0	1	0	0	0	0	0	0	0
52	5	2	0	0	2	0	0	0	0	0	0	0
53	5	6	0	3	0	0	0	0	0	0	0	0
54	1	2	2	0	1	0	0	0	0	0	0	0
55	0	0	0	0	1	0	0	0	0	0	0	0
56	0	0	4	3	13	0	0	0	0	0	0	0
57	1	1	5	0	0	0	0	0	0	0	0	0
58	2	2	4	1	7	0	0	0	0	0	0	0
59	0	1	1	0	0	0	0	0	0	0	0	0
60	0	0	1	0	1	0	0	0	0	0	0	0
61	2	1	2	0	2	0	0	0	0	0	0	0
62	0	1	0	0	1	0	0	0	0	0	0	0
63	0	0	1	0	0	0	0	0	0	0	0	0
64	1	0	0	0	2	0	0	0	0	0	0	0
65	1	0	2	0	4	0	0	0	0	0	0	0
66	0	0	0	0	1	0	0	0	0	0	0	0
67	3	3	0	0	0	0	0	0	0	0	0	0
68	1	0	0	0	0	0	0	0	0	0	0	0
69	1	0	0	0	1	0	0	0	0	0	0	0
70	2	0	0	0	1	0	0	0	0	0	0	0
71	0	1	0	0	1	0	0	0	0	0	0	0
72	1	2	0	0	0	0	0	0	0	0	0	0
73	0	0	2	2	0	0	0	0	0	0	0	0
74	0	1	0	0	1	0	0	0	0	0	0	0
75	7	1	3	0	7	0	0	0	0	0	0	0
76	15	2	14	1	7	0	1	0	0	0	0	0
77	0	0	1	2	2	0	0	0	0	0	0	0
78	0	0	0	0	1	0	0	0	0	0	0	0
79	0	2	2	0	2	0	0	0	0	0	0	0

DATA TABLE 3.—*Silwood delta fragment areas per quadrat*

Stand	<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Salix cinerea</i>	<i>Ilex</i>	<i>Aesculus</i>	<i>Acer</i>	<i>Crataegus</i>	<i>Typha</i>	<i>Nuphar</i>	<i>Salix, Alba</i>
1	30.5	22.5	---	---	5.0	---	---	---	---	---	185.0	---
2	28.0	3.5	---	0.5	---	2.5	---	---	---	---	---	---
3	68.5	---	1.0	---	0.5	---	---	---	---	---	---	---
4	30.0	4.5	13.5	3.0	2.0	---	15.0	---	---	---	1.0	---
5	92.5	1.0	2.0	1.0	17.5	2.0	---	---	0.5	0.5	---	---
6	91.0	3.5	36.0	38.0	20.0	20.5	---	1.0	---	1.0	---	---
7	110.5	---	24.5	42.0	23.0	4.5	2.5	1.0	---	0.5	---	---
8	299.0	20.0	88.5	77.0	48.5	14.0	4.5	0.5	3.0	19.5	---	---
9	161.0	6.5	9.0	4.0	6.0	1.0	---	---	---	51.0	---	---
10	628.0	43.0	---	4.0	51.0	7.5	3.0	---	3.5	36.0	---	---
11	173.5	24.5	---	5.5	48.0	3.0	---	---	---	13.0	---	---
12	80.5	19.0	---	3.5	7.5	---	1.5	---	---	4.0	---	---
13	614.5	32.0	1.5	21.0	41.0	4.0	---	---	---	19.0	---	20.5
14	351.0	12.5	---	0.5	24.0	1.5	---	1.0	---	17.5	---	5.5
15	423.5	3.5	---	32.5	3.0	1.5	---	---	---	2.5	---	---
16	215.5	50.5	---	11.5	4.0	---	---	---	---	3.5	---	28.5
17	43.0	13.5	49.5	---	4.0	---	49.5	---	---	3.0	4.5	---
18	9.0	---	---	---	---	---	---	---	---	---	2.5	---
19	38.0	2.0	---	---	0.5	---	---	---	---	---	---	---
20	97.5	---	---	3.0	---	3.0	54.0	---	---	2.5	1.5	---
21	14.0	---	6.5	9.0	12.0	8.0	---	---	---	2.0	1.0	---
22	40.5	0.5	33.5	8.5	11.0	5.0	7.5	---	1.5	---	0.5	---
23	210.5	---	28.0	31.0	7.0	3.5	---	---	---	---	7.5	---
24	22.0	1.5	23.5	---	5.0	3.0	---	---	---	---	21.5	---
25	206.0	2.0	27.0	56.5	14.0	22.0	---	---	---	4.0	---	---
26	22.5	1.5	17.0	---	7.5	7.5	---	---	---	1.5	---	---
27	448.5	45.0	5.0	42.5	91.0	5.0	1.5	---	---	18.5	---	18.5
28	66.0	---	---	---	1.0	---	---	---	---	2.5	---	---
29	60.5	4.5	0.5	2.0	15.0	---	---	---	---	---	---	---
30	40.5	---	0.5	1.5	4.5	1.0	---	---	---	1.5	---	---
31	108.0	16.0	---	0.5	8.5	---	---	---	---	5.5	---	---
32	118.5	11.0	9.0	22.0	3.0	5.0	---	---	---	4.0	---	---
33	180.0	13.0	10.0	2.0	42.5	3.5	---	---	---	5.0	0.5	5.0
34	266.5	---	---	---	---	---	---	---	---	14.5	---	4.0
35	170.5	4.5	---	0.5	2.0	1.5	---	---	---	3.5	---	---
36	137.5	19.5	---	1.0	8.0	2.0	---	---	---	3.0	---	---
37	75.0	8.0	---	2.0	---	---	---	---	---	3.0	1.0	---
38	81.0	6.0	---	0.5	0.5	---	---	---	---	3.0	---	---
39	45.5	1.0	1.5	4.5	3.0	---	44.5	---	---	---	---	---
40	21.0	---	---	4.0	---	---	---	---	---	---	---	---
41	68.0	10.0	72.0	70.0	98.5	8.5	---	0.5	0.5	---	---	---
42	27.0	3.0	13.5	18.5	2.0	7.5	---	---	---	---	---	---
43	21.0	9.0	12.5	9.0	22.0	3.5	1.5	---	---	1.0	---	1.0
44	17.5	11.5	---	4.5	6.0	---	---	---	---	2.0	---	---
45	195.0	22.0	14.0	23.0	18.0	4.5	---	---	---	13.5	---	---
46	21.0	0.5	9.5	3.0	2.0	1.5	---	---	---	1.0	---	---
47	109.0	18.5	74.5	0.5	6.5	1.0	---	---	---	2.0	---	---
48	22.5	12.0	---	5.0	10.5	1.5	---	---	---	1.5	---	---
49	81.5	0.5	0.5	3.0	3.5	2.0	---	---	---	1.5	---	---
50	22.5	14.0	0.5	2.5	1.5	---	---	---	---	---	---	---
51	42.5	5.5	1.5	4.5	0.5	10.0	---	---	---	6.0	1.0	---
52	---	16.0	---	1.0	0.5	---	---	---	---	1.5	---	---
53	105.0	2.5	---	---	---	0.5	---	---	---	5.0	---	---
54	74.5	14.5	---	---	0.5	---	---	---	---	5.5	0.5	---
55	4.0	1.0	---	1.5	2.0	---	---	---	---	0.5	---	---
56	75.0	---	53.0	98.5	95.5	3.5	---	---	1.0	---	---	2.5
57	28.5	3.0	6.0	2.5	0.5	4.0	---	---	---	---	---	---
58	60.5	4.5	10.0	26.0	6.5	---	27.5	---	---	---	---	---
59	28.5	6.5	61.0	35.5	7.5	3.0	---	---	---	5.5	1.0	---
60	16.0	---	1.5	2.5	1.5	---	---	---	---	0.5	---	---
61	54.0	9.0	1.5	3.5	2.5	3.0	---	---	---	2.0	---	---
62	9.0	2.5	8.5	1.0	6.0	---	---	---	---	---	---	---
63	43.5	0.5	1.0	---	---	---	---	---	---	---	---	---
64	6.0	---	2.5	3.0	1.5	0.5	---	---	---	---	---	---
65	12.5	9.5	1.0	4.5	9.0	---	---	---	---	---	---	---
66	102.0	---	---	19.5	3.0	0.5	---	---	---	---	6.0	---
67	92.0	9.0	---	1.0	8.0	---	---	---	---	---	---	---
68	31.5	---	---	---	1.0	---	---	---	---	---	---	---
69	11.0	9.0	2.0	0.5	1.5	0.5	---	---	---	18.5	---	---
70	4.0	0.5	4.5	3.0	2.5	1.0	---	---	---	5.0	---	---
71	23.0	---	5.0	20.0	9.0	6.0	---	---	---	1.0	---	---
72	2.5	1.0	0.5	3.0	0.5	1.0	---	5.0	---	---	---	---
73	3.5	---	1.5	8.0	0.5	1.0	---	---	---	---	---	---
74	27.5	7.0	14.0	16.5	9.0	3.5	---	---	---	---	---	---
75	32.0	1.0	1.0	2.5	0.5	3.5	---	---	---	---	---	---
76	186.5	28.5	24.5	10.0	14.5	3.0	21.5	---	---	1.0	---	---
77	32.0	8.0	8.0	3.0	2.0	1.5	---	---	---	5.0	---	---
78	8.5	7.0	0.5	1.5	4.0	---	---	---	---	---	---	---
79	6.5	4.0	2.0	12.0	6.0	2.5	---	1.5	---	---	---	---

DATA TABLE 4.—*Silwood delta total area of whole leaves per quadrat*

Stand	<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Salix cinerea</i>	<i>Ilex</i>	<i>Aesculus</i>	<i>Acer</i>	<i>Crataegus</i>	<i>Typha</i>	<i>Nuphar</i>	<i>Salix, Alba</i>
1	564.0	190.0	216.5	62.0	208.5	---	124.5	---	---	---	---	---
2	37.0	5.0	58.0	34.0	11.5	---	53.5	---	---	---	---	---
3	70.0	6.0	---	---	6.0	---	53.0	---	---	---	---	---
4	30.5	9.0	167.0	---	12.5	---	---	---	---	---	---	---
5	134.0	---	8.5	---	8.5	---	---	---	---	---	---	---
6	183.5	7.5	44.0	13.5	28.5	---	---	---	---	---	---	---
7	180.0	3.5	---	---	26.5	---	2.5	---	---	---	---	---
8	462.0	83.5	131.5	7.0	155.0	---	5.0	---	---	---	---	---
9	415.5	---	---	---	39.5	---	---	---	---	---	---	9.0
10	134.1	54.0	5.5	49.0	97.0	6.5	---	---	3.5	---	---	31.5
11	331.5	16.5	---	20.0	43.0	---	---	---	---	---	---	---
12	954.0	134.0	---	10.0	125.5	---	---	---	2.5	---	---	16.0
13	263.0	46.0	7.0	68.0	31.5	---	---	---	---	---	---	---
14	634.0	28.5	7.5	46.0	9.5	9.0	---	---	---	---	---	---
15	906.5	111.0	---	139.0	27.5	---	---	---	---	---	---	53.0
16	820.0	59.5	---	---	18.5	---	---	---	1.0	---	---	---
17	259.0	7.5	121.0	6.0	33.5	---	71.0	---	---	---	---	---
18	25.5	0.5	76.5	---	---	1.5	---	---	---	---	---	---
19	59.5	---	37.5	---	12.0	---	---	---	---	---	---	---
20	14.0	1.0	179.0	---	---	---	---	---	---	---	---	---
21	2.0	6.0	---	---	15.5	---	---	---	---	---	---	---
22	5.0	---	14.5	2.0	1.5	---	---	---	---	---	---	---
23	9.5	---	63.5	---	10.0	---	---	---	---	---	---	---
24	32.0	3.5	---	---	1.0	---	---	---	---	---	---	---
25	199.5	20.5	39.5	22.0	135.0	11.0	---	---	---	---	---	---
26	92.0	15.5	23.0	---	55.5	---	---	---	8.0	---	---	---
27	638.5	21.5	---	77.0	128.0	---	---	---	---	---	---	---
28	12.0	---	---	---	16.0	---	---	---	---	---	---	---
29	21.5	2.0	---	4.5	5.0	---	---	---	---	---	---	---
30	34.0	2.0	---	15.0	15.0	2.5	---	---	---	---	---	---
31	96.5	8.0	---	50.5	47.0	---	---	---	---	---	---	---
32	172.5	4.0	---	---	12.0	---	---	---	---	---	---	---
33	398.5	22.5	---	28.0	39.5	---	---	---	---	---	---	11.5
34	309.5	5.0	25.5	---	---	---	---	---	---	---	---	19.5
35	267.0	14.0	---	---	0.5	---	---	---	---	---	---	---
36	75.0	5.5	---	---	2.5	---	---	---	---	---	---	---
37	119.0	40.0	---	---	7.5	---	---	---	---	---	---	---
38	95.0	10.0	---	---	---	---	---	---	---	---	---	---
39	46.5	---	91.5	18.5	7.5	---	---	---	---	---	---	---
40	---	---	12.0	---	---	---	---	---	---	---	---	---
41	86.0	16.0	48.5	44.0	170.0	---	---	---	---	---	---	---
42	---	---	---	---	12.0	---	---	---	---	---	---	---
43	---	---	19.0	---	6.5	---	---	---	---	---	---	1.5
44	---	4.0	---	20.5	9.5	---	---	---	---	---	---	---
45	241.5	20.0	144.5	25.5	1.5	---	---	---	---	---	---	---
46	6.5	---	17.0	---	---	---	---	---	---	---	---	---
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	13.0	---	4.5	7.0	---	---	---	---	---	---	---
51	64.0	---	17.5	---	0.5	---	---	---	---	---	---	---
52	70.5	19.5	---	---	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	48.5	---	---	---	---	---	---	---
57	36.0	3.5	37.5	---	---	---	---	---	---	---	---	---
58	28.5	---	47.0	4.0	10.5	---	---	---	---	---	---	1.5
59	---	6.0	4.5	---	---	---	---	---	---	---	---	---
60	---	---	27.0	---	4.5	---	---	---	---	---	---	---
61	17.5	18.0	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	50.0	18.5	---	---	---	---	---	---	---	---	---	---
68	44.0	---	---	---	---	---	---	---	---	---	---	---
69	1.0	---	---	---	1.0	---	---	---	---	---	---	---
70	26.5	---	---	---	7.5	---	---	---	---	---	---	---
71	---	1.5	---	---	0.5	---	---	---	---	---	---	---
72	3.5	6.0	---	---	---	---	---	---	---	---	---	---
73	---	---	15.5	29.0	---	---	---	---	---	---	---	---
74	---	3.0	---	---	0.5	---	---	---	---	---	---	---
75	116.0	3.5	46.0	---	25.0	---	13.5	---	---	---	---	---
76	251.0	10.0	212.5	23.0	32.5	---	39.5	---	---	---	---	---
77	---	---	4.5	61.5	13.0	---	---	---	---	---	---	---
78	---	---	---	---	0.5	---	---	---	---	---	---	---
79	---	12.5	31.0	---	3.5	---	---	---	---	---	---	---

DATA TABLE 5.—*Silwood delta area of all leaf material per quadrat*

Stand	<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Salix cinerea</i>	<i>Ilex</i>	<i>Aesculus</i>	<i>Acer</i>	<i>Crataegus</i>	<i>Typha</i>	<i>Nuphar</i>	<i>Salix, Alba</i>
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	13.5	180.5	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	11.5	80.0	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	9.0	42.5	21.5	1.0	---	---	---	51.0	---	9.0
10	1970.0	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	38.0	0.0	1.5	---	---	4.0	---	---
13	1568.0	166.0	1.5	31.0	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	1330.0	14.5	---	171.5	30.5	1.5	---	---	---	2.5	---	53.0
16	1035.0	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	16.0	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	220.0	---	91.5	31.0	17.0	3.5	---	---	---	---	7.5	---
24	405.5	22.5	66.5	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	---	63.0	7.5	---	---	8.0	1.5	---	---
27	1087.0	66.5	5.0	119.5	219.0	5.0	1.5	---	---	18.5	---	18.5
28	78.0	---	---	17.0	---	---	---	---	---	2.5	---	---
29	82.0	6.5	0.5	6.5	20.0	---	---	---	---	---	---	---
30	74.5	2.0	0.5	16.5	19.5	3.5	---	---	---	1.5	---	---
31	204.5	24.0	---	51.0	55.5	---	---	---	---	5.5	---	---
32	291.0	15.0	9.0	22.0	15.0	5.0	---	---	---	4.0	---	---
33	578.5	35.5	10.0	30.0	82.0	3.5	---	---	---	5.0	0.5	16.5
34	576.0	5.0	25.5	---	---	---	---	---	---	14.5	---	23.5
35	437.5	18.5	---	0.5	7.0	1.5	---	---	---	3.5	---	---
36	212.5	25.0	---	1.0	10.5	2.0	---	---	---	3.0	---	---
37	194.0	48.0	---	2.0	7.5	---	---	---	---	3.0	---	---
38	176.0	16.0	---	0.5	0.5	---	---	---	---	3.0	1.0	---
39	92.0	1.0	93.0	4.5	3.0	---	44.5	---	---	---	---	---
40	21.0	---	12.0	4.0	---	---	---	---	---	---	---	---
41	154.0	26.0	120.5	86.0	268.5	8.5	0.5	---	0.5	---	---	---
42	27.0	3.0	13.5	18.5	14.0	7.5	---	---	---	---	---	---
43	---	---	19.0	---	---	---	---	---	---	---	---	1.5
44	---	4.0	---	20.5	9.5	---	---	---	---	---	---	---
45	436.5	42.0	158.5	48.5	6.0	4.5	---	---	---	14.5	---	---
46	27.5	0.5	26.5	3.0	1.5	1.5	---	---	---	1.0	---	---
47	121.0	49.5	124.5	0.5	23.5	1.0	---	---	---	2.0	---	---
48	34.0	28.5	---	19.5	16.0	1.5	---	---	---	1.5	---	---
49	105.0	9.0	0.5	3.0	16.0	2.0	---	---	---	1.5	---	---
50	62.0	27.0	0.5	7.0	8.5	---	---	---	---	---	---	---
51	106.5	5.5	19.0	4.5	1.0	10.0	---	---	---	6.0	1.0	---
52	70.5	35.5	---	1.0	9.0	---	---	---	---	1.5	---	---
53	70.5	46.0	---	75.5	---	0.5	---	---	---	5.0	---	---
54	93.5	15.5	39.5	---	2.5	---	---	---	---	5.5	0.5	---
55	4.0	1.0	---	1.5	3.0	---	---	---	---	0.5	---	---
56	128.0	---	97.0	138.0	144.0	3.5	---	---	1.0	---	---	2.5
57	64.5	6.5	43.5	2.5	0.5	4.0	---	---	---	---	---	---
58	89.0	4.5	57.0	30.0	17.0	---	27.5	---	---	---	---	1.5
59	28.5	12.5	65.5	35.5	7.5	3.0	---	---	---	5.5	1.0	---
60	16.0	---	28.5	2.5	6.0	---	---	---	---	0.5	---	---
61	71.5	27.0	33.5	3.5	9.5	3.0	---	---	---	2.0	---	---
62	9.0	8.5	8.5	1.0	10.5	---	---	---	---	---	---	---
63	43.5	0.5	16.0	---	---	---	---	---	---	---	---	---
64	8.0	---	2.5	3.0	9.5	0.5	---	---	---	---	---	---
65	45.0	22.0	1.0	---	18.0	---	---	---	---	---	---	---
66	102.0	---	---	19.5	7.5	0.5	---	---	---	---	6.0	---
67	142.0	27.5	---	1.0	8.0	---	---	---	---	---	---	---
68	75.5	---	---	1.0	---	---	---	---	---	---	---	---
69	12.0	9.0	2.0	0.5	2.5	0.5	---	---	---	18.5	---	---
70	30.5	0.5	4.5	3.0	10.0	1.0	---	---	---	5.0	---	---
71	23.5	1.5	5.0	20.0	9.5	6.0	---	---	---	1.0	---	---
72	6.0	7.0	0.5	---	0.5	1.0	---	5.0	---	---	---	---
73	3.5	---	17.0	37.0	0.5	1.0	---	---	---	---	---	---
74	27.5	10.0	14.0	16.5	9.5	3.5	---	---	---	---	---	---
75	148.0	4.5	47.0	2.5	25.5	3.5	13.5	---	---	---	---	---
76	437.5	38.5	237.0	33.0	47.0	3.0	61.0	---	---	1.0	---	---
77	32.0	8.0	12.5	64.5	15.0	1.5	---	---	---	5.0	---	---
78	8.5	7.0	0.5	1.5	4.5	---	---	---	---	---	---	---
79	6.5	16.5	33.0	12.0	9.5	2.5	---	---	---	---	---	---

