PROBLEMS IN THE RECOGNITION OF PLANT COMMUNITIES IN POLLEN DIAGRAMS

by

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In recent years pollen analysis has turned increasingly from historical plant geography towards paleoecology. More and more the main interest lies in a reconstruction of the past vegetation instead of simply floristics of a region.

Vegetation as a rule is made up of communities [1]) that can be described quantitatively in terms of species composition or qualitatively in terms of structure.

Concepts of what a community is and how it can be adequately described differ widely, but it may be stated that by pollen analysis any reconstruction of a past vegetation involves primarily species composition.

Likewise in comparison of fossil and recent vegetation the easiest reference can be made to communities that are defined primarily by species composition.

The emphasis on the total ecosystem is accompanied by a renewed study of other microfossils and macrofossils (cf. WEST, 1964). Such integrated studies are highly useful in the reconstruction of the environment. Among those are especially the studies at Lake Windermere and Estwaite Water, in the English Lake district, where pollen diatoms, Cladocera and pigments were analysed. Similar integrated studies have been carried out in Denmark, Sweden, Germany and the U.S.A. All these studies have one thing in common: they deal with particles that are not dispersed by wind. If we do not consider secondary deposition, the presence of these organisms in sediments means also local occurrence i.e. they all belong to one community. Thus the source of the microfossils is no problem.

On the other hand the local occurrence of these fossils means also that there is no even sorting before deposition. This prevents us

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[1]) The term plant community is used here in its widest sense. It comprises any combination of species that thrive together in a particular kind of environment.

from drawing a statistically valid sample from the population. Consequently there is generally no constant proportion between the quantity of fossil and recent types.

Quite different is the situation in pollen analysis. Pollen grains are dispersed by air and a sample from this homogeneous mass of pollen grains may be statistically valid.

THE QUANTITATIVE APPROACH

RECONSTRUCTION OF THE VEGETATION BY THE AMOUNT OF POLLEN TYPES

It has often been stated in the literature that the proportions of pollen types found in a sample do not reflect the real composition of the vegetation, because the relative abundance of pollen types is determined by pollen production and dispersal. In order to arrive at an idea what proportion exists between the composition of the vegetation and the corresponding pollen count, surface samples may be taken from surficial sediments, or pollen may be trapped, in a region with a known vegetation. This proportion may be expressed in a so called R-value (DAVIS, 1963; TSUKADA, 1958; CURTIS, 1959). These R-values may be applied to fossil pollen assemblages. FAEGRI (1966), however, is of the opinion that R-values change from point to point, because of the differential dispersion of pollen grains. If this is true, then each site would have its own characteristic deposition of pollen rain, and one would meet severe problems in the characterization of vegetation types by their pollen count. Surface sample studies, however, indicate that when local and long distance pollen types are omitted one may find a similar pollen count at any place within any region that is characterized by an overall vegetation type (e.g. formation) (e.g. WENNER, 1947; LICHTI-FEDEROVICH & RITCHIE, 1965; McANDREWS, 1966; GRICHUK, 1968; JANSSEN, 1966; POTTER & ROWLEY, 1960).

This may be explained by the following model (fig. 1). As a rule the components of a large vegetation unit are not completely homogeneously distributed, but the individual smaller vegetation types often are patterned and repeat themselves over and over again. In fig. 1 we have similar stands A, B, C, ... D, each of which constitutes a source area. Such a source area, which consists of numerous sources close together may be considered as a single source. An analogous system is described by LUCAS (1958/59): over a city there is an initial build up of the concentration of SO_2 but then the concentration remains constant as the SO_2 dissolves in fog particles, which then descent to the ground. In fig. 1 the following four assumptions have been made:
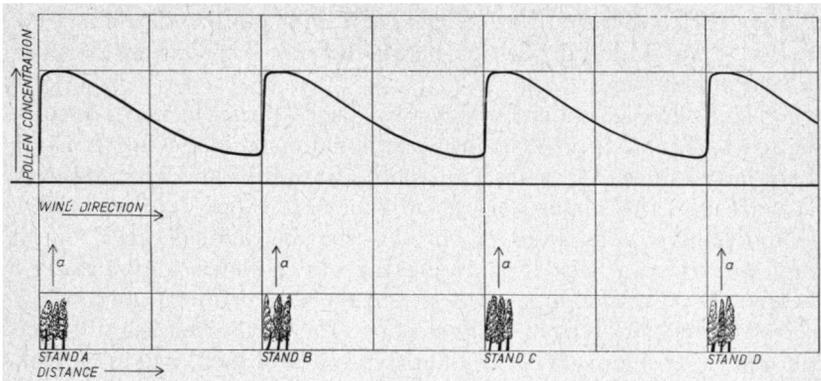
Fig. 1. Pollen dispersal over a large vegetation unit. For explanation see text.

1. There is an average wind direction and wind force blowing from the left. All other atmospheric conditions are also constant.
2. Stands A, B, C, ... D are regularly spaced and not too close together.
3. Each stand produces similar amounts of pollen grains.
4. Pollen samples are collected far enough from the source to produce a regional pollen deposition in the sence I used earlier (JANSSEN, 1966).

Suppose that above stand A we have a concentration of pollen grains of a, then towards the right the pollen concentration decreases to a' with increasing distance. Above stand B we have again a concentration a from stand B (production of A, B.. are equal) plus what is still in the air from stand A thus a+a'. Above stand C there is a concentration of a+a'+a'' and above D a concentration of a+a'+a''+a'''.

In these additions only the first terms will contribute considerably to the concentration of pollen grains. The last terms are small and may be omitted from the equation. This means that after an initial increase on the windward side of the large vegetation type, the dispersion curve will become saw-toothed and will fluctuate between two constant upper and lower concentration levels. How large these fluctuations are is determined for example by the spacing of the stands and by atmospheric conditions. If TAUBERS rain-out component is discarded then theoretic examples may be calculated with SUTTONS (1953) formula of dispersion. This however is not the object of this paper.

Of course when there is a discontinuity in the vegetation then additional sources will not be available anymore, and the dispersion curve will decrease very rapidly. The phenomenon described above

may be the reason that large vegetation units can be characterized by a regional pollen deposition in which there is a constant proportion of pollen types.

Surface samples collected in known vegetational formations subsequently can be applied to interpret fossil assemblages in terms of these large units (MCANDREWS, 1966). An additional advantage is that areas of the major vegetation types are often determined by geomorphology, and their extent can then be defined easily. They may be used as a basis for interpreting past pollen assemblages.

Apart from the regional deposition, there is also local deposition as well as deposition from other regions. The local effect usually does not pose a problem. Which pollen types are of local origin can be traced by an investigation of the macrofossils in the parent material. Also the extralocal effect (cf. JANSSEN, 1966) is negligible when the size of the basin is not too small. But the deposition from outside the overall region often causes problems, especially when the regional deposition is low as is often the case in non-forested areas. In these cases additional diagrams should be constructed in which pollen types from elements outside the area are eliminated from the percentage calculation.

There are indications that the decline of the dispersion curve for most pollen types is sufficiently sharp to separate regions by their regional pollen content, not only at a short distance from the source where local values decrease rapidly to regional values (JANSSEN, 1966) but also farther away when no additional pollen sources are available. This also agrees with TAUBERS theoretical considerations (TAUBER, 1965: 23—27). Samples from adjacent formations of different composition still remain clearly different in their pollen composition. TRAUTMAN (1957) for instance reported in Germany a difference in the proportion of *Fagus* and *Quercus* in the older Subatlantic at two sites that are ca 10 km apart. One site was situated in an acidophilous *Fagus-Quercus* region, another at the border of this region and an area covered by more mesic *Fagus* forests. WATTS (1960) demonstrated in Ireland similar differences in pollen composition in the Subboreal within about 30 km in four major vegetation units which were determined by strong geological contrasts. Likewise SMITH (1964) reported different kinds of pollen diagrams from sites 5 km apart from two regions characterized by different soil conditions (Fallahogy-Cannons Lough).

Also MCANDREWS (1966) shows this in both surface samples and stratigraphic diagrams.

Apparently if the regional pollen deposition is large enough the influence of pollen from outside the region does not affect the regional pollen assemblage to a wide extent, especially in the absence of pine. If pine pollen is present in considerable percentages then it

often will prove difficult to decide whether the pine pollen grains come from a few trees within the region of from whole stands at a distance. The same problem may arise for other elements when their pollen productivity is very high in relation to the regional average.

The question remains, however, whether or not pollen percentages from fossil assemblages should be converted or not. I agree with FAEGRI (1966) that application of correction factors does not give information that is not present in the original count. Moreover, within certain limits R-values change from one vegetation type to another due to variations in the pattern of vegetation and consequently in pollen dispersal (JANSSEN 1967a). It may be more useful to construct auxiliary diagrams, eleminating pollen types that are grossly overrepresented in one way or another.

THE QUALITATIVE APPROACH

RECONSTRUCTION OF THE VEGETATION BY MEANS OF POLLEN INDICATORS

Plant species tend to grow together in definite combinations, depending on the living and non living environment. In this way each pollen type found in the sediments indicates "something" about the environment, and it points to the possible presence of other ecologically related taxa. Already in 1931 this was recognized by TÜXEN in his paper: "Grundlagen der Urlandschaftforschung", in which he proposed to interpret pollen diagrams by separating the vegetation in space on the basis of soil differences in- and outside an imaginary valley. TÜXEN drew vegetation maps in various periods of the Holocene on the basis of the present occurrence of communities on these soils.

Indicator species are often minor constituents of the vegetation and the probability of finding pollen grains from these species in the regional pollen deposition is low. This applies especially to forests where the forest bottom vegetation is very underrepresented in the total pollen deposition. Moreover, in the regional deposition one often does not know where the pollen comes from. But in the local pollen deposition the resolution among the pollen types can be high. Strictly, a quantitative representation of these types in a diagram does not make any more sense than a representation for other kinds of local organisms. On the other hand, the differentiation of types is so exact that one may infer the composition of a fossil vegetation.

The still rather scant data on the history of recent communities as determined on the basis of a combination of species indicate that

they all originate from the late Holocene, many of them not earlier
then the advent of man. According to ZOLLER (1962) the Querco-
abietetum sphagnetosum arose in medieval times. WILLERDING
(1960) concluded from pollen, seed and wood analyses that his
Subatlantic and Medieval assemblages of species belong to quite a
few discrete communities that are also present today (e.g. Biden-
tion tripartiti, Scheuchzerio-Caricetalia etc.). OPRAVIL
(1961) traced by wood analyses the Quercion pubescentis
back to the Halstatt period and SLAVIKOVA (1960) did the same for
Tilieto-Acerion and Taxeto-Fagetum.

The Ericetum tetralices, according to MENKE's (1963) study
of pollen and macrofossils was present already in the Subboreal
although not connected with man. In contrast the Valeriano
dioica-Caricetum davallianae is of Medieval origin in
Czechoslovakia. (MORAVEC & RYBNICKOBA, 1964). Also the
Juncetum gerardi, the Scripetum maritimi, and other
communities are traceable to the early Subatlantic according to
seed analysis of KÖRBER-GROHNE (1967). The Rhynchosporion
albae and Valerianeto-Filipendulatum were probably
present in the Subboreal and especially the Subatlantic periods
(JANSSEN, 1960). GROSSE-BRAUCKMANN (1967) investigated the
macrofossils content of peats in northwestern Germany and found
compositions that are equivalent to our recent Phragmitetalia,
Caricetalia fuscae, and other communities. But also deviations
from the present types were found, such as mixtures of ombrotrophic
and minerotrophic species.

LÜDI (1954) found that almost all species of the Neolithic dwelling
placed in Switzerland are still present in the region. He concluded
that thus communities in the Neolithic were similar to the recent
ones.

A similar pattern seems to exist in part of the lowland commu-
nities in North America. The ecological amplitudes of some species
involved in the process lake filling were probable similar in at
least the Subboreal and Subatlantic (JANSSEN, 1967).

If we arrange the pollen types in a diagram in ecologic groups,
then successions of plant communities are most easily visualized (e.g.
IVERSEN, 1959; ANDERSEN, 1964; BERGLUND, 1966; JANSSEN, 1967;
also in seed diagrams: WATTS & WINTER, 1966).

Thus it appears that recent plant communities cannot usually be
traced beyond the Subboreal period. In Europe this is not surprising
since most of the vegetation is anthropogenous. It applies probably
for many of the present main vegetation types in northwestern
Europe, for instance the Calluneto-Genistetum, even in places
where it most likely would be a natural vegetation type (SW Sweden:
FRIES, 1959), the Querceto-Betuletum (TRAUTMAN, 1962;

FIRBAS, 1954) [1]) or *Picea* forests in the Sudeten (RYBNICKOVA, 1966), and even in Finland (VASARI, 1965). Usually we believe that these communities arose by the influence of man on the basis of the rise of one pollen type only, (usually the dominant type), combined with the occurrence of culture indicators. In such cases when only part of the whole assemblage points to a certain vegetation type, it may be possible that the fossil vegetation type had another species composition.

One may ask whether the recent ecologic groups existed in the same way in the early Holocene. There are indications that the composition of species of these older vegetation types was different from that of recent ones. Some examples may illustrate this. In central and south-central Europe *Fagus sylvatica* and *Abies alba* have similar ecological requirements. In south-central Europe they constitute a distinct community and a belt well defined altitudinal in the mountains. In many pollen diagrams their curves increase simultaneously in the Subboreal, and one may be inclined to state that this community migrated as an entity. Yet, according to ZOLLER & KLEIBER (1967) south of the Alps *Abies* appears already in the Preboreal and Boreal periods. Much later, after *Picea* immigrated during the Atlantic, *Fagus* appears in the Subboreal, giving rise to the present Luzulo- and Eu-Fagion communities.

Similar problems in the early Holocene exist in northwestern Europe in the interpretation of the role of *Corylus* (cf. e.g. LANG, 1967) and in North America in the reconstruction of the vegetation of the *Pinus resinosa/banksiana* assemblage zone (MCANDREWS, 1966; JANSSEN, 1967). For a discussion of late glacial pollen assemblages in this connection see IVERSEN (1954, 1964) or CUSHING (1963: 137).

In swamp vegetation we have similar problems. The pollen assemblage of swamps in the southern Netherlands in the early Holocene, thus before the arrival of the edaphic climax species *Alnus glutinosa*, shows a composition unknown today (unpubl. material). LANG (1967) reports from the Late-glacial in SW Germany an assemblage of both eutrophic and oligotrophic species. A similar situation is present in the early Holocene of Minnesota (JANSSEN, 1967). KATZ & KATZ (1964) even report in the Riss-Würm interglacial *Scheuchzeria* associated with eutrophic mosses. They doubt the existence of true raised bogs in preholocene periods. Also POP (1964, 1967) is of the opinion that our present raised bog flora comes from heterogeneous sites, especially from eutrophic fens.

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[1]) According to FAEGRI (1939/1940) in western Norway a Querceto-Betuletum occurred already in the Subboreal, although it was not identical with this recent community (higher *Corylus* frequences in the Subboreal).

There are three main reasons why a comparison with recent plant communities fails to be productive.

1. Most authors point to competition. Ecologic groups are often in reality sociological groups (SCAMONI & PASSARGE, 1959) which include the factor of competition. Recent plant communities are composed of various phytogeographic elements, among which are immigration elements and, (HEIMANS, 1939) mesochorous elements. In the early Holocene several species had not yet migrated into the area, resulting in different competitional conditions and thus other species combinations (cf. also IVERSEN, 1960).
   Alternatively (FAEGRI: in LANG, 1967) absence of competition in pioneer vegetation may be the reason for the broad ecological amplitudes observed for many species of the Late-glacial. CUSHING (1965) favors the use of autecology rather than ecological groups. The drawback may be that the autecology of many species is not well understood and that it does not account for the factor of competition.

2. According to ANDERSEN (1964), differentiation of soils occurred late in the Holocene. In this way species that are now restricted to acid soils once may have occurred on neutral soils, together with species that also today occur on these soils.

3. The more we go back in time the more there is chance that other ecotypes are involved (cf. IVERSEN, 1964; FIRBAS 1949).
   In spite of this, the application of recent ecologic groups sometimes works surprisingly well even in pre-Holocene periods.
   Examples may be found for the Late-glacial (ANDERSEN, 1961) for the lake flora and terrestrial vegetation of the Eemian interglacial (ANDERSEN, 1964, 1966) and for the Pliocene (ZAGWIJN, 1967). They show that, despite possible different or broader ecological amplitudes our present ecologic groups can be meaningful entities sometimes also before the last few thousand years. We have indeed no choice. ZOLLER (in LANG, 1967) points to the principle of actuality that should be the basis of any ecologic interpretation.

All in all the conclusion must be that the use of pollen types as indicators of vegetation types works for the later part of the Holocene with a flora not too different from the present one. Before the Atlantic period the application of the present ecological tolerances of species may be of doubtful value. In these cases deductions from the quantitative approach, comparing percentages of pollen types in surface samples and those in diagrams, may be more productive.

THE COMPOSITION OF THE POLLEN SUM

In the recognition of plant communities in pollen diagrams the selection of the pollen sum is one of the most important consequences. Many authors (e.g. FAEGRI, 1966; FAEGRI & IVERSEN, 1964; WRIGHT & PATTEN, 1963) have already dealt with this aspect extensively. Only a few remarks may suffice. Any pollen sum presupposes an ecologic identity and thus has a bearing on a vegetation type (e.g. the forest-tree pollen sum of VON POST or the upland pollen sum of IVERSEN (1942). In selecting a pollen sum one has to determine which vegetation type produced certain pollen types. Thus if we want to consider the total vegetation in a region everything has to be included, at least in so far as we are dealing with true regional deposition. If part of the vegetation is the main interest the sum may be adjusted accordingly. In principal a special pollen sum for visualizing succession in any vegetation type is justified, though not often practical. The main reason to exclude a number of pollen types is the phenomenon of local occurrence. Because the pollen mixture of local types is quite heterogeneous a statistically valid sample from such a population is impossible. For that reason a special pollen sum for local vegetation types is impractical. There are two possibilities for the local types

1. A calculation based upon the regional pollen sum but without the inclusion of the local types. According to FAEGRI (1966) this does not make much sense neither geobotanically nor statistically. These types should be omitted alltogether. This may be true but often it is desirable to have any measure of relative abundance of the local types, despite the fact that the calculation basis is not constant. For instance, if there is in a pollen diagram a change from local to regional values, this might show up quite nicely in the curves even if they are excluded from the sum.

2. Another possibility is a calculation after individual inclusion in the regional pollen sum (e.g. in TROELS-SMITH, 1955). For the smaller percentages it does not matter very much which method is followed. But it makes a difference for larger amounts of local types. Individual inclusion in the sum tends to diminish the fluctuations of high percentages of these types, the extreme character of which is often an indication of local occurrence. The first method therefore may be still preferable despite its drawbacks.

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