

A palaeoecological model for the interpretation of wild plant species

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Received June 26, 1995 / Accepted October 24, 1995

Abstract. The interpretation of subfossil records of wild plant species with respect to both environmental conditions and past vegetation is complicated by the following: (1) production and dispersal of plant remains including diaspores, (2) the formation of the soil flora, (3) taphonomic processes and differential preservation that act on subfossil assemblages and (4) methods applied to produce subfossil records. Whereas the similarity between recent plant communities and seed banks is often weak, the relationship between past vegetation and subfossil assemblages is still more complicated. It is therefore unlikely that macrofossil assemblages derived from soil samples can be considered as pure samples representing particular palaeobiocoenoses. The assumption that plant communities, in the past, may have been in some way aberrant with respect to composition and that the ecological ranges of species varied during the Quaternary has to be rejected, if not based on well considered assumptions or evidence from pure samples. Only if a sufficient number of suitable studies is available, which enable evaluation between all kinds of plant communities and their respective seed floras, can progress be made with regard to the reconstruction of past vegetation and environmental conditions. As long as these data are not available, the ecological interpretation of particular subfossil assemblages isolated from soil samples has to be carefully evaluated within their particular context.

Key words: Palaeobotany – Palaeoenvironment – Seed bank – Plant macrofossils – Plant communities

Palaeobotany: a general model

Palaeobotanical research in an ecological context

Ecologists investigating soil seed banks have much in common with palaeobotanists. Both aim at linking seeds in the soil to the above-ground vegetation. Ecological research is mainly concentrated on the analysis of the

living seeds in the soil in connection with vegetation dynamics and management or restoration of vegetation (Leck et al. 1989). Palaeobotanists aim at interpreting botanical analyses of samples with respect to ancient economic systems, past environmental conditions and past vegetation (e.g. Körber-Grohne 1967; Van Zeist 1974; Behre 1976). Archaeological samples may contain almost pure organic deposits of, for example, threshing remains or grains in storage pits, but more often the samples contain much soil along with seeds and other plant remains. In both cases, the ecological interpretation of wild plant species is hampered by several processes that act on the botanical remains in the course of time, starting with seed production in former plant communities and ending with the compiling of subfossil records. These processes are part of topical areas of research by plant ecologists and so there is an abundance of relevant information available regarding the ecological interpretation of subfossil records. The use of these data by palaeobotanists, however, is limited. For example, palaeobotanical reports dealing with the ecological interpretation of waterlogged remains of wild plant species only rarely refer to studies dealing with recent soil seed banks (e.g. Jensen 1987; Küster 1991). The limited use can be explained by the status quo of knowledge, in which the availability of standardized information is a crucial fact, and also by the level of integration of both palaeobotany and ecology.

A contribution to the integration of both these disciplines is obtained by unifying relevant concepts used by palaeobotanists and ecologists in one model (Fig. 1). This model is particularly applicable to the ecological interpretation of subfossil remains of wild plant species present in soil samples. With the help of this model it is possible to define the main problems that are encountered when interpreting these records. It can also be used to illustrate the methods of investigation used by 'green ecologists', so that their results can be coupled with those of the palaeobotanical researches. Two different kinds of concepts are presented in the model: those that are structural in character and those that deal with processes; examples of the former are placed in boxes.

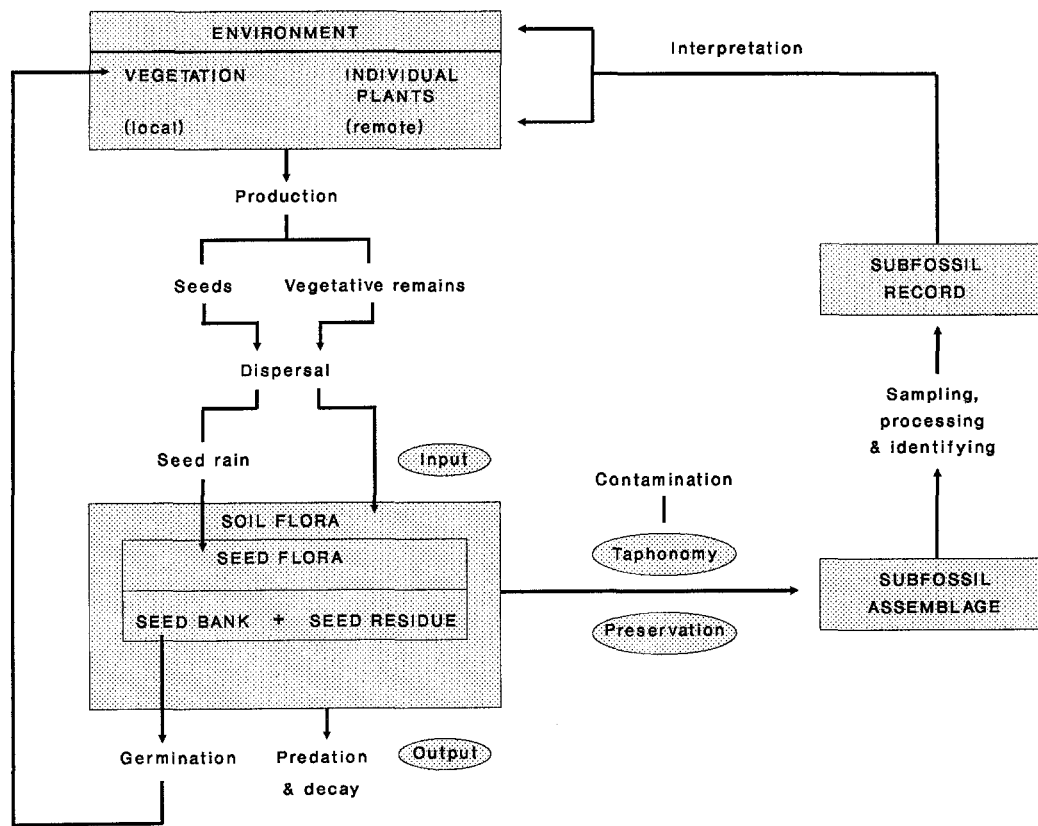


Fig. 1. Palaeoecological model for the interpretation of plant macro-remains from soil samples

In this study the term 'palaeobotany' is used when botanical remains from either natural sediments or ancient settlements are dealt with. The term 'archaeo-botany' refers to the analysis of botanical remains from settlement sites, whereas the term 'palaeoethnobotany' is reserved for the interpretation of plants in connection with human activity. First some remarks will be made on the structural concepts and then the various processes will be discussed.

Structural concepts

Although botanical remains in the soil reflect to some extent above-ground plants, they cannot be labelled with the same concept. Established plants can be organized into a hierarchical classification of vegetation types based on their floristic composition. The validity of these classifications, as compared to seed bank classifications, is determined by environmental requirements of the species with regard to germination and seedling establishment. Seeds in the soil comprise both viable and non-viable seeds. The soil seed bank is defined as all viable seeds present on or in the soil or associated litter (Simpson et al. 1989). The term 'seeds' is used here in a popular sense and includes all kinds of diaspores. Non-viable seeds in the soil and associated litter are referred to as 'seed residue', whereas the term 'seed flora' is introduced for the combination of seed bank and seed residue. Because the composition of seed assemblages only partly

correlates with environmental characteristics, the more general concept 'flora' is chosen. This definition differs from the one used by Major and Pyott (1966) who include viable seeds in the soil with the flora, but fits in with Greig (1988) referring to subfossil plant assemblages from wells as 'well floras'. Although vegetative remains are easily fragmented and are less suited to become preserved, they may also contribute to the palaeobotanical record. The total number of plant remains in the soil is, therefore, encompassed by the general concept 'soil flora'.

A second use of the concept of 'seed bank' concerns a typology on the level of individual plant species with respect to the fate of their seeds. As to the temperate regions, Thompson and Grime (1979) distinguished four different seed bank types in relation to seed longevity, which in turn is correlated with germination physiology. These four types can be clustered in two main types: transient seed banks and persistent seed banks. Species with transient seed banks produce seeds that remain viable for only one year. Persistent seed banks are characterized by seeds that can become dormant and may remain viable for several years, especially if incorporated into the soil. Recently, Thompson et al. (1993) separated the persistent seed bank into two categories, which is relevant for purposes of nature management but not useful for palaeobotany.

The above-mentioned concepts with respect to the botanical remains in the soil are all applicable to the analysis of recent soil contents. As to subfossil plant re-

mains, the terms 'subfossil assemblage' and 'subfossil record' are used. The subfossil assemblage is a derivative of the soil flora and can be considered as the target population being sampled. The actual list of plant species recovered is the sampled population and will be referred to as 'subfossil record'. It is emphasized that subfossil seed assemblages may reflect more than just a part of the seed residue. Some species like members of *Chenopodium* and *Atriplex* have very decay-resistant seed coats and may, therefore, become part of the subfossil record even if they have germinated in the distant past.

Input and output to the soil flora

The input of botanical remains into the soil, in which the term 'seed rain' is used for generative propagules, depends on production and dispersal. The seed production shows a high variability both within and between species and is determined by variables such as reproductive allocation and effort (Bazzaz and Ackerly 1992), pollination failure (Fenner 1985) and pre-dispersal seed predation (Crawley 1992). A main distinction concerns the reproduction by means of seeds and by means of vegetative organs. This may be illustrated by the difference in seed production in *Holcus mollis* and *H. lanatus*. The annual *H. lanatus* reproduces exclusively by seeds. In the case of the perennial *H. mollis*, which is capable of spreading by tillers over large areas, seeds are seldom found. This difference is also reflected in subfossil records (Körber-Grohne 1990). On a smaller scale, allocation is also performed by the trade-off between seed size and number, depending upon the life history and habitat of species (Silvertown 1982). Dioecism appears to be of minor importance. Common dioecious species such as *Silene dioica*, *Urtica dioica*, *Cirsium arvense* and *Rumex acetosella* are well represented in subfossil records.

Seed shadows of many species show that a high percentage of the seeds is primarily dispersed within short distances of the parent plant. Curves that describe the distribution of seeds at increasing distances from the seed source, are often leptokurtic, with a higher peak and longer tail than normal distribution (Willson 1992). Nevertheless, long-distance dispersal may result in the loss of seeds from the plant community. On the same basis, seeds from remote species may invade communities under study. The same is true for vegetative remains, though they are especially transported by water due to the lack of special dispersal devices (Rich 1989; Spicer 1989).

The loss of seeds may often be the result of germination, predation and decay. Germination will reduce the seed bank, whereas predation and decay may affect both seed bank and seed residue. Because the identification of macro-remains also includes fragments, these losses are only partly valid in an archaeological context.

Preservation

The prevention of a further breakdown of plant remains by decomposers is a necessary condition for becoming part of the subfossil assemblage. Several types of preser-

vation are possible: charring, waterlogging, mineralization and desiccation. Also imprints in pottery may indirectly maintain the presence of a species in the course of time. The type of preservation depends on environmental conditions and human activity.

Charring as a mode of preservation may be the result of natural causes like lightning and of human interference by means of accidental or deliberate fire, such as cooking, heating and burning rubbish. Charred plant remains are preserved in both wet and dry soils and may in principle be applicable to all kind of species. However, archaeobotanical records show evidence that weeds and ruderal species are preserved more frequently by charring than water plants and semi-helophytic species are. Moreover, charring is destructive in character as a result of which the remains of certain species may be destroyed (Wilson 1984; Bottema 1984).

Waterlogging is not destructive in character but is, like charring, a selective mode of preservation too. Firstly, waterlogged remains are poorly or generally not preserved in open sites with a moist to dry soil (Miksicek 1987). Secondly, plant remains differ in all kind of characteristics, such as hard-seededness, moisture content and impermeability of the seed coat, which make them partly suitable for this type of preservation. In this respect, differences in seed dispersal and seed bank type are of special interest. Dispersal can occur in both space and time. The dispersal strategy of certain species is adapted to survival at the same locality. Seeds are dispersed close to the parent plant and longevity and dormancy of the seeds make it possible that germination is inhibited for a long span of time. This strategy is a common phenomenon of many arable weeds and ruderals. However, this picture may become somewhat complex for members of families that produce polymorphic seeds, such as Chenopodiaceae, Cruciferae, Compositae, Leguminosae and Gramineae (Harper et al. 1970; Sorensen 1978; Silvertown 1984). Polymorphic seeds originating from the same individual plant show differences in dispersal and germination. For example, a combination of dispersal in space and time could be demonstrated for *Senecio jacobaea* (McEvoy 1984).

Species that have (partly) adapted to dispersal in time and that have (long-term) persistent seed banks are assumed to have better chances of becoming preserved by waterlogging than species that have transient seeds and have adapted to dispersal in space. Seeds of species of the first group must sustain environmental hazards during the long period of time they remain viable in the soil. Adaptations that support this longevity may also be favourable to preservation by waterlogging. Unfortunately, standardized information on dispersal strategies, longevity, dormancy and seed bank types for complete floras has as yet not been available. This kind of information would certainly contribute towards the understanding of selective preservation of seeds during time spans exceeding those of interest to vegetation dynamics in modern ecology.

Some examples may support this assumption. Greig (1984), who studied the botanical composition of samples from recent hay meadows, found that some species such as *Plantago lanceolata*, which produces transient

seeds, together with many grasses were very well represented by seeds in fresh samples, while they are relatively scarcely preserved by macro-remains in an archaeological context. From an examination of subfossil Gramineae fruits of the Netherlands, Northern France, Belgium, Germany and Switzerland, it could be demonstrated that some species characteristic of modern meadows are not, viz. *Trisetum flavescens* and *Bromus erectus*, or are only scarcely preserved by waterlogging, viz. *Alopecurus pratensis* and *Arrhenatherum elatius* (Körber-Grohne 1990). From *T. flavescens*, *A. pratensis* and *A. elatius*, which are common species in the Netherlands today, no buried or persistent seed bank has yet been reported (Grime et al. 1988). It is plausible that the type of seed bank may partly explain their absence. Moreover, artificial fossilisation of modern fruits of *T. flavescens* proved to be very difficult (Körber-Grohne 1991). The linkage of seed bank type and chance of preservation is, however, not unambiguous. For example, subfossil fruits of *Festuca rubra* are frequently found despite their transient seeds. The fruit walls of the waterlogged specimens are relatively thick and mostly well preserved. From other common grasses with a transient seed bank, such as *Dactylis glomerata*, *Lolium perenne* and *Cynosurus cristatus*, the waterlogged fruits are scarcely preserved and the thin envelopes of the last two species are mostly eroded.

Taphonomy

Taphonomy deals with processes that act on organisms after death (Gifford 1981). Taphonomic processes have especially been studied with respect to the formation of assemblages of (sub)fossil animal remains. The incorporation of seeds and fruits into the soil follows naturally from the ultimate fate of diaspores. Therefore, taphonomic studies concerning plant remains are primarily focused on vegetative plant parts (e.g. Rich 1989; Spicer 1989).

Taphonomic processes are linked with dispersal and preservation of plant remains and sedimentation. Strictly spoken, dispersal and sedimentation also affect viable seeds and the demarcation with respect to taphonomy is, therefore, somewhat arbitrary.

Special attention should be given to dispersal which results in mixtures of plant remains of different ages. This contamination does not apply to admixtures as a result of contemporaneous dispersal and accumulation of seeds from successional stages. Two types of contamination can be distinguished. Subfossil assemblages may have become contaminated with much older fossil remains and subfossil remains may have become mixed with recent plant parts. Wind and water, in particular, can be considered as important agencies for the first type of contamination. For example, rivers and sea currents may dissect old deposits and thereby mobilize subfossil or even fossil plant remains. In a study of recent drift litter samples of the Netherlands, several examples of contamination could be demonstrated (Cappers 1993). Carboniferous megaspores were found in samples along the River Rhine as well as along the Dutch coast and

probably originated from upstream tributaries dissecting carboniferous sediments in the Ruhr area of western Germany. In the same study, reference is made of the occurrence of an endocarp of the species *Potamogeton filiformis* in a sample of the Dutch terp (dwelling mound) Ouddorp, located in the province of Zeeland. This species is extinct in the Netherlands and is only known from Pleistocene deposits. Its occurrence in a sample dated to the second century A.D. can be explained by the deposition of tidal marks on the slope of this dwelling mound in the past. This process is still active, as can be seen by the rounded peat fragments washed ashore and originating from dissected peat layers in the bottom of the North Sea Basin. On a smaller scale, humans may also be responsible for this kind of contamination. The use of sods of peat for fires may result in the preservation of associated species by charring.

Modern contamination, on the other hand, may concern procedural contamination which can be prevented by careful sampling and by checking seed rain during the excavation (Keepax 1977; Minnis 1981). On a smaller scale, the activity of animals may be responsible for contamination so that seeds may be transported in both upward and downward directions (Hurka and Haase 1982).

Sampling, processing and identifying

The degree to which the ultimate subfossil record will represent the subfossil assemblage depends on sampling strategies, processing methods and identification skills. The sampling method involves the selection of contexts, distribution of samples over the area and sample volumes. Some contexts like ditches and ruderal places developed their own specific seed flora in addition to secondary waste disposal by humans. Other contexts, such as storage pits, primarily served for the deposition of supplies and may only secondarily have been filled with remains of wild plant species. Selection of contexts will, therefore, influence the composition of the records. For example, pits of sites in northern France investigated by Bakels (1984) yielded variable amounts of charred remains. In those cases where the number of wild plant species was large, an environmental interpretation could be made despite the artificial character of the context and its mixed origin. Especially the storage pits of the Suippes area (Marne department) proved to be fruitful. They yielded a reasonable number of species, including those indicative of calcareous soils and representing fields, grasslands, ruderal areas and forest edges.

Deposition of supplies, threshing remains, faeces and the like, which are strongly correlated with cultivated plants, are mostly well recognized during the excavation ensuring appropriate sampling. Seeds of wild plant species not associated with these kinds of deposits, may be unevenly scattered over the area. Studies dealing with recent seed banks of natural vegetation frequently revealed clustered patterns both horizontally and vertically in the soil and make it advisable to collect many small samples in order to obtain a more representative record of species (e.g. Thompson 1986; Dessaint et al. 1991). The validity of this recommendation as to archaeo-bo-

tanical research is demonstrated by the excavation of the Dutch Neolithic settlement of Swifterbant (Van Zeist and Palfenier-Vegter 1983). Because no distinct activity areas were visible during the excavation, it was initially decided to sample each square metre per 10 cm layer. On the basis of the botanical richness, a final selection was made of the quadrants from which a three litre sample was examined. It turned out that concentrations of seeds could be clearly distinguished. The minimum volume of a sample that has to be looked through in order to reveal the majority of species present, is often estimated from species-volume curves (Hutchings 1986). Considering the clustered distribution of naturally dispersed seeds, however, it is recommended to spread the labour intensive analyses over small samples representative of the area.

The recovery technique and choices concerning the identification will also influence the selection of seeds assembled in the sample. This may apply to sieves that to some extent determine the type of species being recovered. A further selection may be performed by the investigator, who is guided by experience in the identification of particular plant remains and the composition of reference collections.

Interpretation of vegetation

The interpretation of subfossil records can either be focused on human-plant relationships or on the ecology of wild plant species. The palaeoecological model is fixed on the latter, in which a further distinction will be made between vegetation and environment. In this section the relationship between the seed flora and the above-ground vegetation will be discussed with respect to both recent and subfossil seed assemblages.

Many studies indicated that strong dissimilarities between recent seed bank and standing vegetation can exist (Leck et al. 1989). This discrepancy may apply to both qualitative and quantitative comparisons. Dominant species in the vegetation may be underrepresented or even completely absent in the seed bank, whereas dominant species in the seed bank may be poorly represented or even absent in the established vegetation. This dissimilarity is connected with biological processes and research conditions. Biological processes concern seed production and dispersal, governing the input into the seed bank on the one hand, and germination, predation and decay that cause the loss of seeds on the other. As for research conditions, the results are much biased by the sampling procedure and the method by which species are detected.

Research conditions that affect the outcome are the sampling design and the time of sampling. Patchiness of seed concentrations in both horizontal and vertical directions makes it necessary to collect many samples. Additionally, the analysis of the seed rain will elucidate the contribution of long-distance dispersal. Time and frequency of sampling have to be geared to seed production and germination.

The composition of the seed bank can be determined in two different ways: the germination assay and the sieving method, each with its own advantages and disad-

vantages. In 66% of the seed bank studies, the seedling emergence method is applied (Brown 1992). A main disadvantage of this analysis is that dormancy of seeds may strongly bias the outcome. Species differ in the way dormancy is broken and it is difficult to anticipate these different conditions without having knowledge of the species composition. Dormancy will also result in delayed germination whereby representatives of several successional stages may be encountered. Even if these methodological problems are taken into account by optimizing the sampling procedure, a dissimilarity between the composition of the seed bank and the vegetation may still be encountered with and can be explained by biological processes (e.g. Brown 1992; Beatty 1991; Bernhardt 1993).

The interpretation of subfossil plant assemblages aimed at the reconstruction of past vegetation is very problematic if plant remains are taken from soil samples in particular. Many samples prove to contain a mixture of species that do not match present compositions of plant communities. According to Van der Veen (1992), two opposing views may explain this phenomenon of charred seed assemblages. Firstly, the sample represents a mixture of different origins; secondly, the sample is primarily made up of species from one single plant community. Thus, the presence of grassland and wetland species in assemblages representing mainly plant communities of arable weeds, should indicate that the composition of past arable weed communities were very different from today's.

It is obvious that the composition of plant communities may have changed in the course of time. This is especially true for anthropogenic communities (Behre and Jacomet 1991). For example, agricultural activity has transformed the environment and consequently associations of crop weeds have evolved (Groenman-van Waateringe 1979; Willerding 1986). However, the question is: on what basis may it be concluded that aberrant species within an assemblage are considered to belong to the same vegetation?

To unravel the assemblages in separate plant communities or to conclude that they represent past vegetations of different species composition, one should take various considerations into account. The presence of aberrant species can also be explained by the invasion of remote species. Moreover, members of different successional stages may be present in the same assemblage, depending on sedimentation rates and contamination processes. On the other hand, species may be missing from assemblages due to differences in seed production, seed dispersal and selective preservation. For example, Palczyński (1992) demonstrated that the seed production in plants of lowland mires depends on the specific plant community in which they grow and also that the numbers did not correspond with quantitative data of subfossil records.

In this respect, some terms are of interest that were introduced in archaeobotanical research and deal with the purity of the source of species within samples. Willerding (1991) distinguishes 'palaeobiocoenoses' and 'thanatocoenoses'. A palaeobiocoenose represents an assemblage of species formed in the place they once occurred and which would mirror the past vegetation.

Given this meaning, the term 'palaeophytocoenose' may be more appropriate. Due to preservation and dispersal, however, the species composition may have been reduced to some degree. Depending on relocation, the palaeobiocoenose is either autochthonous in character, as with a culture layer along a lake or allochthonous in character as with a dung layer on a terp. Körber-Grohne (1967) labelled samples according to the degree of purity, in which pure samples ("*reine Proben*") were not mixed with plant remains of other origins. A thanatocoenose, on the other hand, is a mixture of species that originally did not grow together.

Obviously, these labels would have only a relative meaning, as analyses of recent soil samples have revealed that the species composition only partly resembles the standing vegetation. Therefore, it is very unlikely that soil samples from an archaeological context would represent just one single plant community. Körber-Grohne (1967) demonstrated that pure samples could only be obtained if they were small and consisted of plant remains only. This is especially true for samples which were dominated by stem fragments of *Juncus gerardi* representing the Juncetum gerardii typicum with dominance of *Festuca rubra*. In pure samples of the subassociations with *Trifolium repens*, however, the number of species rises from c. 15-20 (typicum) to c. 40 species, including species that would have originated from neighbouring plant communities, such as *Salicornia europaea*, *Brassica rapa* and *Potamogeton lucens*.

Interpretation of the environment

Plants are adapted to specific environmental conditions and hence are tools by which the environment can be characterized. Indicator values have been assigned to species as to edaphic and climatic factors and are available for both vascular plants and mosses in Central Europe (Ellenberg et al. 1991) and the Netherlands (Runhaar et al. 1987; Van der Meijden et al. 1991; Dirkse and Kruijssen 1993). The main advantage of the indicator values determined for the Netherlands is that they take account of the ecological range of species.

The methodological objections with respect to the reconstruction of past vegetation also apply to the characterization of past environmental conditions. Two different methods have been developed. So-called ecodiagrams are constructed in which the distribution of species with respect to a certain environmental factor is visualized, whereby in principle all available species are taken into account (Willerding 1978, 1980). In the second approach a selected number of indicator taxa is used whereby changes in representativeness can be analysed (Behre 1991; Brinkkemper 1993; Cappars 1994). Both indicator values and indicator species are suitable for the comparison of subfossil records on different levels, for which samples can be clustered according to differences in time, space or feature types.

A disadvantage of characterizing past environments by means of indicator values is the absence of a frame of reference. A comparison between subfossil records may

demonstrate shifts in the ecological conditions in the course of the occupation of a particular site, but it is not possible to interpret the absolute numbers of plant remains recorded. This can only be done if distributions of subfossil records at a site are compared with those of more wide-ranging subfossil and recent floras (Cappars 1995). These floras may comprise a whole country, but may also be limited to a smaller area. In this way, bias in the subfossil records becomes clear, thus enabling a more meaningful interpretation.

Implications for palaeobotanical research

Uniformitarian assumptions

A necessary condition for the interpretation of past events is the assumption that these events can be explained in terms of present-day processes and relationships. This principle is known as 'uniformitarianism' and is also designated by the term 'actualism' (Gifford 1981; Roberts 1989).

The ecological interpretation of subfossil records has more validity for the environmental characterization than for the composition of plant communities. From the palaeoecological model (Fig. 1) it is clear that the interpretation of subfossil records by means of reconstructing specific species compositions of past vegetations has to be rejected if not based on considered assumptions or pure samples. The comparison of subfossil records with present-day classification systems of vegetation types as an alternative is valid, but has some disadvantages. Firstly, the composition of a specific vegetation in relation to its environment is variable and depends on seed dispersal, ecological range and competition of species. Consequently, character species may be lacking in a specific relevé whereas other species are mentioned as companions. In an archaeological context, this may be even more confusing if, for various reasons, character species are poorly represented in subfossil records. Secondly, the increasing influence of human activity on the environment has resulted in shifts in the composition of plant communities, as is particularly demonstrated for weed associations (e.g. Willerding 1986) and grasslands (e.g. Körber-Grohne 1990). In this respect, Körber-Grohne is not in favour of naming prehistoric and early historical vegetations after plant species which at that time had not yet occurred, e.g. the classes Molinietalia and Arrhenatheretalia for the period from the Neolithic until the Middle Ages.

The uniformitarian assumption in palaeoecology, which claims that the ecological preference and tolerance have not changed through time, is likely to be more valid. According to Behre and Jacomet (1991) this assumption may be true for the whole of the Quaternary. As a consequence, it seems acceptable that species have invaded only those habitats in which the specific environmental conditions are within the physiological limits of the species concerned.

The use of indicator values is, however, limited to some extent. First, they are based on recent field observations instead of data collected from physiological experiments. Physiological ranges may be broader than

ecological ones. Moreover, the observed ecological ranges depend on the species composition of the plant communities in which the species occur. Shifts in species composition result in different interspecific competitions, which in turn may affect the ecological range of individual species. A second limitation results from the reduction of the ecological range in the indicator values themselves. Even if the ecological range is taken into account, the assumed ecological range is often reduced for practical reasons by the exclusion of relevés that represent isolated situations (Runhaar et al. 1987). The interpretation of subfossil records in terms of environmental conditions is complicated by the fact that part of the seeds incorporated into the soil actually fail to germinate due to the absence of suitable environmental conditions.

A different ecological range is adduced for some species based on palaeobotanical research. On the basis of correspondence analysis carried out on plant macrofossil data from De Horden, province of Utrecht, the Netherlands, which date to the Roman period, Lange (1990) found that, in some instances, *Festuca rubra*, *Lycopus europaeus* and *Stachys palustris* grew under other conditions than expected, i.e. they were partly associated with cereals, weeds and ruderals. The probability of dispersal is, however, not ruled out, so that especially *F. rubra* and *L. europaeus* may still be regarded as non-weedy species.

Another species that is considered to be a weed of arable fields in former times is *Eleocharis palustris* (Jones 1988). Seeds of this plant are frequently found in association with cereal debris which is preserved by charring. It is suggested that in earlier periods *E. palustris* grew in drier habitats, comparable with its occurrence in dry-sown rice fields today. There are, however, alternative explanations for the occurrence of *E. palustris* with cereals, one of them put forward also by Jones. Surface sealing, for instance, makes the soil relatively impermeable to water and is a well-known phenomenon of agricultural soils. Under such conditions, *E. palustris* may have grown in arable fields, but is still indicative of wet soils that could temporarily become dry (Weeda et al. 1994). The presence of seeds of *E. palustris* can be explained as a result of manuring arable fields with mud taken from ditches (Bieleman 1992) or as being carried there by streams that have overflowed into the fields. On the other hand, it is obvious to consider its status as an admixture if only small numbers of seeds of *E. palustris* are found (e.g. Groenman-Van Waateringe and Pals 1983; Kosina 1978). This does not apply to *Danthonia decumbens*, which is also assumed to have been an arable weed in former times (Hillman 1981, 1982). This perennial species could maintain itself as a weed as long as fields were ploughed by ard. In this case, it is a matter of adaptation of life form to agricultural practice just like the successful invasion of *Cyperus esculentus* in maize and potato fields in the Netherlands during the last two decades, due to vegetative propagation by tubers (Mennema 1984).

As long as convincing arguments have not been put forward to reject alternative explanations, the uniformitarian assumption concerning the constancy of ecological preference and tolerance should be maintained in favour of explanations that propose a change in the ecology of a species.

Seed flora studies and scaling

There is an area of tension between processes that determine the composition of a seed flora and the interpretation of subfossil records. Sound knowledge of the ecology of the seed flora is a necessary condition for a detailed interpretation, both for the environmental characteristics and for the vegetation. Unfortunately, studies on seed floras in settlements are scarce, despite the increase of interest in urban ecology (e.g. Köhler 1990).

Within the scope of experimental archaeology, studies dealing with the formation and composition of seed floras are, therefore, of special interest. Thus far, archaeobotanical case studies are focused particularly on the dispersal of botanical remains into settlements through human agency (e.g. Greig 1984; Van Haaster 1989; Van Zeist 1988). The possibility of natural mechanisms that brought plant remains to a site is frequently mentioned but rarely confirmed by empirical data. The study of recent seed floras of various contexts in settlements are therefore recommended and should include the description of the established vegetation and the input of plant remains into the soil. This is the only possible way to gain insight into the composition of subfossil assemblages to such an extent that the interpretation can be confined to relatively small areas and periods, by which possible shifts in species composition and ecological ranges can be taken into account.

As long as sufficient data on the formation of seed floras of settlement areas are not available, the ecological interpretation of particular subfossil assemblages isolated from soil samples has to be adjusted to appropriate scales. Inasmuch as seed floras have spatial and temporal dimensions, this distinction also applies to the ecological interpretation. Both dimensions are determined by sample volume, feature type and botanical richness. Small subsamples that take sedimentation rates into account are more suitable for unequivocal interpretations. Samples that provide many species are more likely to represent different environments and plant communities, and will probably also be influenced by the archaeological context in which they occurred. In particular, the temporal scale will depend on the dating of the sample, the presence of species representing different successional stages and the contamination with plant remains of other periods. The spatial scale, on the other hand, will particularly depend on the possibility that plant remains have been transported over large distances, either by cultural or natural agencies.

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