

An ecological characterization of the Holocene palaeobotanical record of The Netherlands

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SUMMARY

An analysis of ecological groups has been performed on the Dutch Holocene palaeobotanical record excluding wood and pollen data and compared with the recent flora.

Although all ecological groups are represented by plants that are preserved by both waterlogging and charring, this especially concerns plants indicative of ruderal places, arable fields, dry underwood, fresh water and banks. On the level of environmental conditions, it is shown that the representation of the subfossil record is biased by the type of preservation, the archaeological context and the frequency by which plants are found.

For the reconstruction of environmental conditions on the basis of a select number of plants, groups of indicator plants have been compiled for the following (a)biotic characteristics: salinity, moisture regime, nutrient availability, and the structure of vegetation and the stage of succession. These groups are suitable for the comparison of samples and sites with respect to different feature types, locations and periods.

Key-words: ecological groups, environmental characteristics, Holocene, indicator plants, palaeobotany, preservation.

INTRODUCTION

Subfossil plant remains are recovered from both archaeological sites and natural deposits. Usually, samples from those sites appear to contain a reasonable amount of wild plant species. These fossil assemblages can be used to reconstruct former environments. However, the application of knowledge on modern ecological relationships to archaeological data is problematic (Green 1982; Jones, 1988; Küster 1991; Willerding 1991).

Dispersal is a potential source of error for it may cause the absence of certain species in the plant record and, on the other hand, may introduce plant remains from remote sites. The incorporation of plant remains into the soil may in fact be actual all the time. The ultimate chance of becoming preserved in the soil archive (preservation *s.l.*) is influenced by seed production, germination, predation, decay and the type of preservation (e.g. waterlogging, charring, mineralization and imprinting). The fossil

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assemblage may be further biased by the sampling method such as the selection of sites and features, the recovery technique used and the volume examined.

The reconstruction of the environment on the basis of subfossil records may concern the floristic composition and the (a)biotic characteristics. Traditionally, the floristic-sociological approach in Dutch palaeobotanical studies is based on the handbook of plant communities by Westhoff & Den Held (1975). A main objection to this approach is the inconstancy of the composition of plant communities in the course of time. During the Holocene, man has increasingly transformed the landscape and many species will consequently have colonized newly created habitats. Another objection concerns the troublesome diagnostic value of character species, especially for lower syntaxonomic units such as associations (Westhoff & Van der Maarel 1973). Consequently, it is accepted that only a comparison of the subfossil record with recent syntaxa on the level of higher units, starting with alliances is justified. This restraint is not exercised for associations that are assumed to have changed little in the course of time, such as those dominated by halophytic species (Körber-Grohne 1992). The introduction of new syntaxa, applicable to archaeobotanical assemblages, is strongly dissuaded because of its methodological problems (Küster 1991; Van der Veen 1992).

The publication of Ellenberg (1979), which gives a synopsis of both climatic and edaphic indicator values of many vascular plants, has frequently been used for the reconstruction of the environmental conditions. Its utility, however, is criticized because the values are based on Central European conditions and do not take into account the ecological range of species (Van Zeist *et al.* 1986; Wilmanns 1988; Ellenberg *et al.* 1991).

The use of ecological groups with regard to subfossil records was introduced by Behre (1979, 1991). To assess the degree of salinity, Behre compiled two selected groups of species, one consisting of 16 halophytes and the other of 16 glycophytes. The comparison between different sites and periods for changes in salinity was visualized in pie graphs, presenting salinity ratios based on presence/absence of halophytes to glycophytes. This ratio was refined by Brinkkemper (1993), who also took account of the sample frequency.

Two classifications of ecological groups are available for the flora of The Netherlands (Arnolds & Van der Maarel 1979; Runhaar *et al.* 1987). They have been updated in the fourth edition of the *Standard List of the Flora of The Netherlands* (Van der Meijden *et al.* 1991). Because the ecological groups of Runhaar *et al.*, which for convenience will be further mentioned as CML-classification (Centrum voor Milieukunde, Leiden), are constructed on the basis of well defined abiotic and biotic environmental characteristics, they can also be applied to the analyses of subfossil records for each of these characteristics separately. Whereas Ellenberg's values are applicable to plants in Central Europe, the CML-classification is adjusted to The Netherlands. Another advantage of the CML-classification is the fact that each plant species is assigned to as many ecological groups as is necessary to explain two-thirds of its occurrence in The Netherlands, based on ecological literature and about 20 000 relevés of Dutch plant communities (Runhaar *et al.* 1987). Therefore, it is possible to take the ecological range of the species into account. Recently, updated indicator values for mosses and liverworts have become available expressed in both Ellenberg's values (Düll 1991) and the codes of the CML-classification (Dirkse & Kruijsen 1993). It has to be realized that, in an archaeological context, the use of ecological groups that are actually based on recent floristic compositions and landscape structure is somewhat problematic because they may have changed during the Holocene. It is assumed that during this period the

constancy of plant species with reference to environmental demands will have changed less in comparison with the floristic composition. For this reason the ecological ranges of species will be given special attention. The weakness of the CML-classification is that the population differentiation of widespread plant species with ecologically non-exchangeable populations is not taken into account. Moreover, the remaining one-third of the occurrences may occasionally give as much ecological information as the other two-thirds, because the population size is not considered in all classifications and thus, inherently, wrong correlations are made. Consequently, the indicator value of some species may be doubtful, even with respect to The Netherlands.

The aim of this study is to present an ecological characterization of the Holocene palaeobotanical record of The Netherlands on the basis of two national classification systems of ecological groups. Both classification systems are used as a frame of reference for the degree of ecological representativeness of the palaeobotanical record with respect to the recent flora. Differences in preservation and in the methods of recovery will reduce the number of subfossil records, and therefore, may bias the ecological characterization. In this study all species recorded as macrofossils for The Netherlands are, as one sample, compared with the flora that was present in The Netherlands in the middle of the nineteenth century. The following questions are addressed: (i) How representative is the Holocene subfossil record with respect to the type of preservation, archaeological context and frequency of recovery? (ii) Which plant species can be used to compile groups suitable for the evaluation of biotic and abiotic characteristics of former environments?

MATERIALS AND METHODS

The subfossil records

The aim has been to include all published records of subfossil plants in the analyses. However, some publications could not be obtained, while some others had to be excluded because the information about age and location were too vague. Publications include reports on both archaeological excavations and borings in natural deposits. Additionally, unpublished data of Van Zeist were used, including those from Groningen and Peeloo. The publications used are listed in Appendix 1.

The selection of records is based on the following criteria: (i) only vascular plants are included; (ii) the plants have to be represented by generative or vegetative macrofossils, but records based on wood identifications only are excluded; (iii) the identification is certain regardless of the taxonomic level. Records based on merely wood identifications or on pollen analyses were omitted because they have different dispersal properties and were not available as a complete data set. Moreover, pollen analytical data only partly consider taxa that are identified to species level, resulting in sparse information on specific environmental demands.

Standardization of the so-called type-identifications, which are a common practice in palaeobotanical research, was performed to optimize comparison. However, the practical value of these records remains limited because the labelling of problem specimens to a group of taxa is not uniform. Moreover, the clustering of taxa very often results in the enlargement of the ecological range.

Radiocarbon dates were (re)calibrated with the program CAL15 (Van der Plicht 1993). Dates concerning Calais Deposits, Holland Peat and Dunkerque Deposits were

recalibrated on the basis of the periodization published by Roeleveld (1974). Calibrated calendar ages are based on the 2σ (95.4%) confidence interval. The dating of the archaeological periods of the Holocene is based on Van den Broeke *et al.* (in press): Mesolithic Period: 9550–5300/4900 BC; Neolithic Period: 5300/4900–2000 BC; Bronze Age: 2000–800 BC; Iron Age: 800–12 BC; Roman Period: 12 BC–450 AD; Middle Ages: 450–1500 AD; Modern Times: 1500–1850 AD.

Species frequency is expressed as site frequency (SF) or as atlas-square-frequency (ASF). Atlas-squares are 25 km² in area and correspond to the ordnance survey maps of The Netherlands, also used in the *Atlas of the Flora of The Netherlands* (Mennema *et al.* 1980, 1985; Van der Meijden *et al.* 1989).

Analyses dealing with the type of preservation were confined to waterlogged and charred remains because mineralized remains and imprints were relatively small in number. Furthermore, mineralization is highly biased by the type of context, and imprints recorded for The Netherlands are almost limited to cultivated plants.

Recent flora

The selection of the recent flora is based on the *Standard List of the Flora of The Netherlands* 1990 (Van der Meijden *et al.* 1991), which in turn is based on the 21st edition of the *Flora of The Netherlands* (Van der Meijden 1990). Because it was not considered appropriate to compare the subfossil record with the current Dutch flora, plants that appeared in The Netherlands as from 1850 were excluded. With the exception of subspecies of *Scirpus lacustris** and *Zannichellia palustris*, which are frequently mentioned in the subfossil record, all taxa are treated at the species level. In this way the total number of taxa from the *Standard List* was reduced to 1286. Atlas-square-frequencies (ASF) of recent plants are based on the codes for frequency published in the *Standard List*.

Use of the CML-classification

In the CML-classification, all ecological groups are labelled by a unique code of three to five symbols for (a)biotic environmental characteristics (Van der Meijden *et al.* 1990). Some plants are attributed to only one ecological group while others are assigned to several of them. Within each ecological group, plants are classified into two categories on the basis of their ecological range. Plants that were attributed to more than one ecological group are classified in the category of plants with a small or a broad ecological range, depending on the difference between the codes for the particular plant. In this way, the ecological range is dependent on the characterization of the whole habitat type. For example: *Angelica sylvestris* occurs in the following groups: (1) tall herb vegetation on wet soils with moderate nutrient availability; (2) tall herb vegetation on moist soils with moderate nutrient availability; (3) woodland and shrub on wet soils with moderate nutrient availability. Due to the variation in structure of the vegetation and moisture regime, in all three ecological groups this species is placed in the category of broad ecological range (Runhaar *et al.* 1987).

In this study, the combined codes of the ecological groups were split up into the individual symbols for the following environmental characteristics: (1) salinity; (2) structure of vegetation and stage of succession; (3) moisture regime; (4) nutrient

*Nomenclature follows Van der Meijden (1990).

availability and acidity. Each taxon is labelled for all four characteristics separately in such a way that every symbol is attributed only once. In this way, *Angelica sylvestris* was characterized by only one symbol for salinity (i.e. for fresh) and nutrient availability (i.e. for moderate), while it has two symbols for the moisture regime (i.e. for wet and moist) and structure of the vegetation and stage of succession (i.e. for tall herb vegetation and woodland and shrub).

In the CML-classification, each plant is considered to have either a broad or a small ecological range, regardless of the constancy of a specific (a)biotic characteristic. The different approach used in this study, however, results in different combinations of plants for each of the environmental characteristics. Taxa are considered to have a small ecological range for a certain characteristic when they have only one symbol for it. When two or more symbols for a certain characteristic are attributed to a taxon, it is treated as one with a broad ecological range. Thus, *Angelica sylvestris* has a small ecological range with reference to salinity and nutrient availability (and will be counted once for each character in the analyses) and a broad ecological range with reference to moisture regime and structure of the vegetation and stage of succession (and will be counted twice for each character in the analyses).

Indicator plants

The compilation of groups of indicator plants suitable for palaeobotanical records is based on the analysis of the Holocene palaeobotanical record of The Netherlands and the CML-classification of ecological groups. The following criteria were used to select the plants: (i) plants must stand a reasonable chance of being part of the subfossil record; (ii) the identification of botanical remains must not be troublesome; (iii) the number of plants permitting, preference is given to plants not utilized by man; (iv) plants must have a small ecological range with respect to the environmental characteristic concerned and, as much as possible, broad ecological ranges for the other characteristics. In this way, characteristics are prevented from becoming tightly linked with each other.

Each taxon is assigned a taxon weight which is based on sample frequency and expresses the change of being part of a subfossil record. For this analysis, only sites from which more than 25 taxa were recorded were used. The relative sample frequency of each indicator taxon (F_i) is calculated from the formula:

$$F_i = \left(\sum_{t=1}^s \frac{M_{ti}}{M_t} \right) / s \quad (i=1, \dots, m_j) \quad (1)$$

where s is the number of sites, M_{ti} is the number of samples with taxon i from site t , and M_t is the number of samples from site t .

The maximum number of indicator taxa (m_j) for each environmental characteristic is 20, with the exception of semi-aquatic helophytic habitats, which are represented by only 10 species. Within each group of indicator taxa, the character weight for each indicator taxon (W_i) is expressed as an index number, based on the highest relative sample frequency (F_{\max}) in that group:

$$W_i = \frac{F_i}{F_{\max}} \quad (2)$$

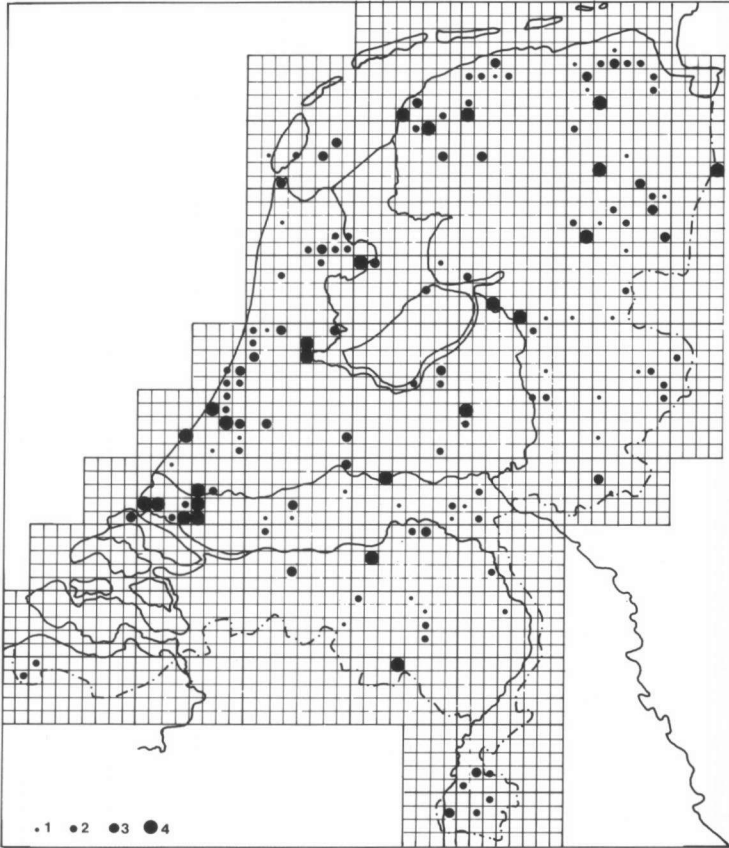


Fig. 1. Distribution of the Holocene subfossil records in The Netherlands. The atlas-square-frequency (ASF) of the taxa is presented in four groups: 1–5 (1), 6–25 (2), 26–100 (3) and >100 (4).

Because the sample frequency is influenced by the type of preservation (see also Bottema 1984; Wilson 1984), different ranges of frequency were calculated separately with respect to waterlogged and charred remains. Some taxa have only been found in a waterlogged condition. In such cases no character weight has been assigned for the charred state of preservation.

RESULTS

Representation in space and time

Although sites from which macrofossils have been used in the analyses show some bias for the coastal area, they are scattered over most of The Netherlands (Fig.1). For the interpretation of the distribution it should be realized that the configuration of the coast-line has changed during the Holocene. The records that have been used in the analyses, are spread over 158 atlas-squares. In 126 atlas-squares, the dots refer only to one site. In the other atlas-squares the records are merged from two (25 atlas-squares) or three (7 atlas-squares) sites. The number of taxa per atlas-square varies from 1 to 247. Atlas-squares with 200 or more taxa enclose the following sites: Dorestad/Wijk bij

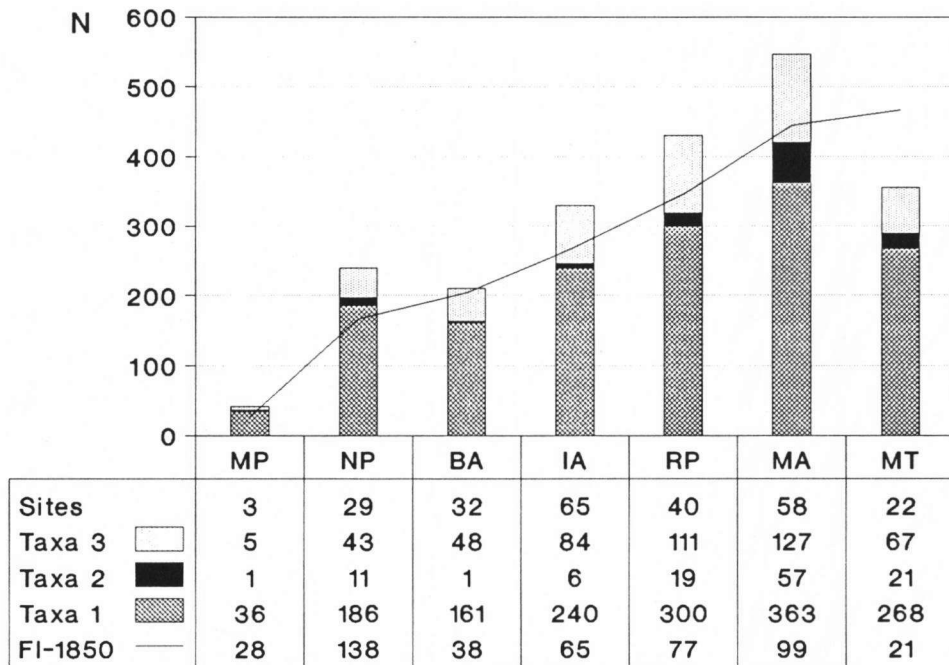


Fig. 2. Number of sites and subfossil taxa recorded for the various periods of the Holocene. Some taxa have been unambiguously identified and are mentioned for at least two different periods (1) or have been mentioned only for the period concerned (2) while other taxa may be considered supplementary, but its assignment is uncertain due to the level of identification (3). The cumulative number of taxa being part of the recent flora (1850) is presented separately (—). Abbreviations for the periods: MP, Mesolithic Period; NP, Neolithic Period; BA, Bronze Age; IA, Iron Age; RP, Roman Period; MA, Middle Ages; MT, Modern Times (1500–1850).

Duurstede/De Horden ($n=247$), Groningen/Paddepoel ($n=241$), Leeuwarden ($n=237$) and Hekelingen/Spijkenisse ($n=200$). Although maps are available for The Netherlands on which the range of the number of taxa per atlas-square is presented (Van der Meijden *et al.* 1989), it is important to realize some basic differences. Firstly, the map of the Holocene subfossil record is based on the sum of records that comprise a much longer period. Secondly, the actual area from which the subfossil records are recovered, is just a fraction of the total area of an atlas-square that is used as a standard area for examining the presence of plants on the basis of field observations.

Thus far, some 650 different taxa have been recorded for the Holocene period. Approximately 75% of these taxa are part of the Dutch flora about 1850, representing it for 36%. Though it is quite difficult to determine the exact amount of taxa that has been recorded for a certain period, mainly due to problem specimens, a particular trend becomes evident (Fig. 2).

There is a decline in the subfossil record for the Bronze Age, which can be explained by the relatively low presence of feature types suitable for the preservation of plant remains, rather than by the number of sites investigated. Medieval settlements, on the contrary, are usually characterized by their favourable conditions for preservation, in particular when feature types are present, such as wells and cesspits, from which many waterlogged remains are recovered. Also *Terpen*, frequently inhabited in late prehistoric (Iron Age) and early historical times, have a name for their rich botanical contents.

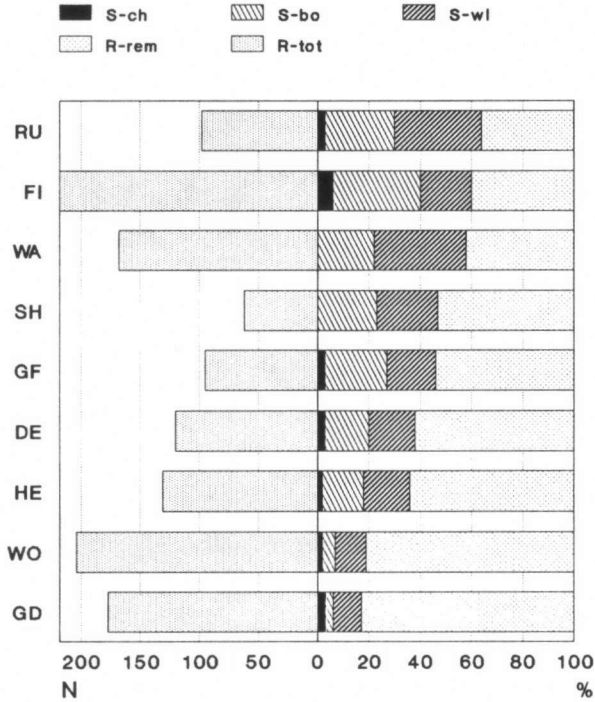


Fig. 3. Representation of the ecological groups for the recent flora and the Holocene subfossil record. The absolute numbers of the recent distributions are shown at the left side (R-tot). At the right side the total amount per ecological group is adjusted to 100% and proportions are shown for the subfossil records and for the remainder taxa of the recent flora (R-rem) not represented in the subfossil records. The subfossil records are divided in waterlogged taxa (S-wl), charred taxa (S-ch) and taxa recorded by both waterlogged and charred remains (S-bo). Abbreviations for the ecological groups: RU, ruderal places or open, moist to wet soils with a low humus content; FI, arable fields and dry underwood; WA, fresh water and banks; SH, dunes, salt water and salt-marshes; GF, fertilized grassland on moist to wet soils with moderate to rich nutrient availability; DE, deforestation, borders and brushwood; HE, heathland, bog, nutrient-poor meadows and chalk marshes; WO, wood; GD, dry grassland and walls.

Taxa that have only been recorded for a specific period are relatively sparse. As far as they form part of the indigenous flora, their single presence can partly be explained by their poor chance of being represented (for example: *Rorippa sylvestris* which has a low seed production is mentioned only for the Mesolithic Period, Van Geel *et al.* 1981). The number of sites and the internationalization of trade routes are responsible for the increase of indigenous as well as exotic plants in the Middle Ages. The ratio of taxa to sites shows that from the Bronze Age onwards every new site, on average, results in the enlargement of the indigenous flora with one to two new taxa.

Ecological groups

The distribution of subfossil plants among the ecological groups distinguished by Arnolds & Van der Maarel (1979) displays a shift as compared with the distribution of recent plants (Fig. 3). More than half of the plants actually growing in ruderal places (RU), arable fields or dry underwood (FI) and fresh water or banks (WA) is also represented in the subfossil record. The first one mentioned comprises only a relatively small number of plants. Not very well represented in the subfossil record are plants growing in woods (WO), in dry grasslands and on walls (GD). The type of preservation

does not carry much weight with the representation of plants in the ecological groups. Plants that have been preserved by both waterlogging and charring or only by waterlogging are represented in all groups. However, the number of taxa of which only charred remains have been recovered is low and even missing for species of fresh water and banks (WA) and dunes, salt water and salt-marshes (SH).

Environmental characteristics

When plants are examined in relationship to their environmental conditions, it is obvious that the ecological range depends on the type of environment (Fig. 4). With respect to salinity, the number of plants with a broad ecological range is low, although they are relatively well represented in the subfossil record due to the number of investigated sites where, in former times, the sea exerted its influence (recent: 5%, and subfossil: 14% of the coded plants). With respect to the other environmental factors, the proportion of taxa with a broad ecological range is considerable: moisture regime (recent: 25%, and subfossil: 42% of the coded plants), nutrient availability and acidity (recent: 34%, and subfossil: 49% of the coded plants) and structure of the vegetation and stage of succession (recent: 22%, and subfossil: 36% of the coded plants). The higher percentages in the subfossil record can be explained by the identification to the level of combinations of species, as a result of which the individual values were joined together. Plants that have not been coded, concern rare and exotic specimens (especially recent records) and combinations of species or genera and family names (especially subfossil records). Because species indicative of saline and brackish environments have not been coded for nutrient availability, the category of not coded species is substantial for the last-named characteristic (Runhaar *et al.* 1987).

When only taxa with a small ecological range are considered, all environments with the exception of low nutrient availability and moderate to high nutrient availability (Fig. 4, LNA-4 and MNA-HNA) are represented. Although most taxa are indicative of fresh water, the halophytic plants are very well represented. With respect to the moisture regime, it is shown that the number of subfossil taxa in proportion to the recent taxa decreases from aquatic to dry habitats. Nutrient availability and acidity as a habitat factor can be subdivided into three classes: (1) low (with a gradient of decreasing acidity: LNA-1 to LNA-4); (2) moderate (MNA); and (3) high nutrient availability (HNA). In particular, environments with a moderate to rich nutrient supply are represented by the subfossil record. Although absolute numbers are small, subfossil taxa indicative of low nutrient supply are particularly frequent for acid conditions proportional to the recent record (Fig. 4, LNA-1). This can be explained by the analysis of macro fossils in association with palynological studies of peat deposits and the use of peat as fuel and its resulting transport to settlements. The distribution of the flora in relation to the classification of vegetation structure and stage of succession shows that pioneer vegetations (including arable weeds and ruderal species), grasslands, shrubs and woodlands are dominant, both for the recent and subfossil record. Plants characteristic of water vegetation and semi-aquatic helophytic vegetation are less frequent, but are proportionally very well represented in the subfossil record. Taxa with a broad ecological range are omitted in further analyses (Figs 5, 6 and 7), because it is not possible to decide which environments they really represent.

The type of preservation causes a shift in the distribution patterns, which is most clearly displayed for plants identified by charred remains (Fig. 5). They particularly represent environments with fresh water and moist soils with a moderate nutrient supply

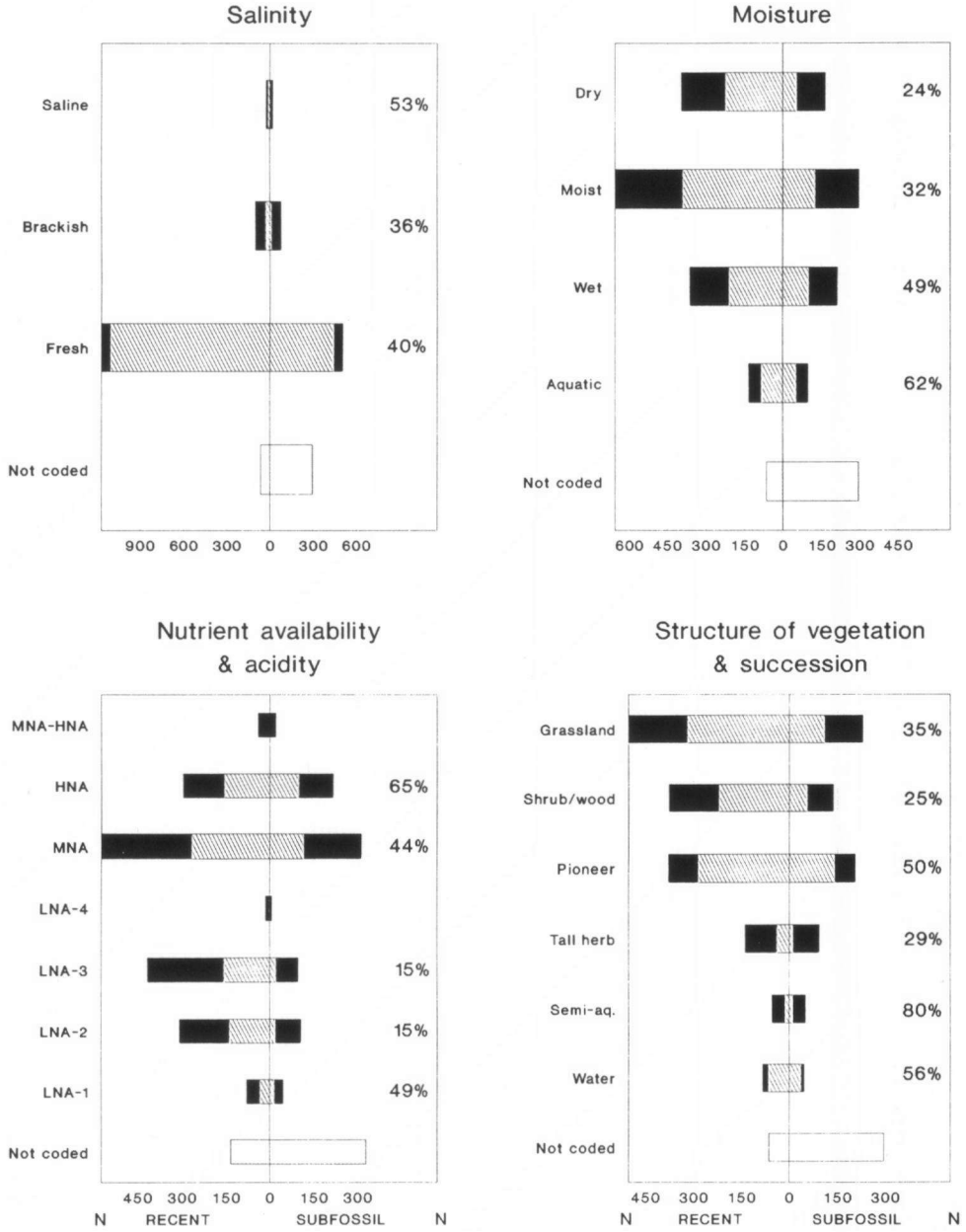


Fig. 4. Distribution of recent (left side) and subfossil taxa (right side) in relation to the four environmental characteristics. Shaded parts concern taxa with a small ecological range, black parts concern taxa with a broad ecological range. Percentages represent the proportion of subfossil taxa with a small ecological range in relation to the recent taxa with a small ecological range. Abbreviations for nutrient availability and acidity: LNA-1, low nutrient avail., acid; LNA-2, idem, moderately acid to neutral; LNA-3, idem, basic; LNA-4, low nutrient avail.; MNA, moderate nutrient avail.; HNA, high nutrient avail.; MNA-HNA, moderate to high nutrient avail.

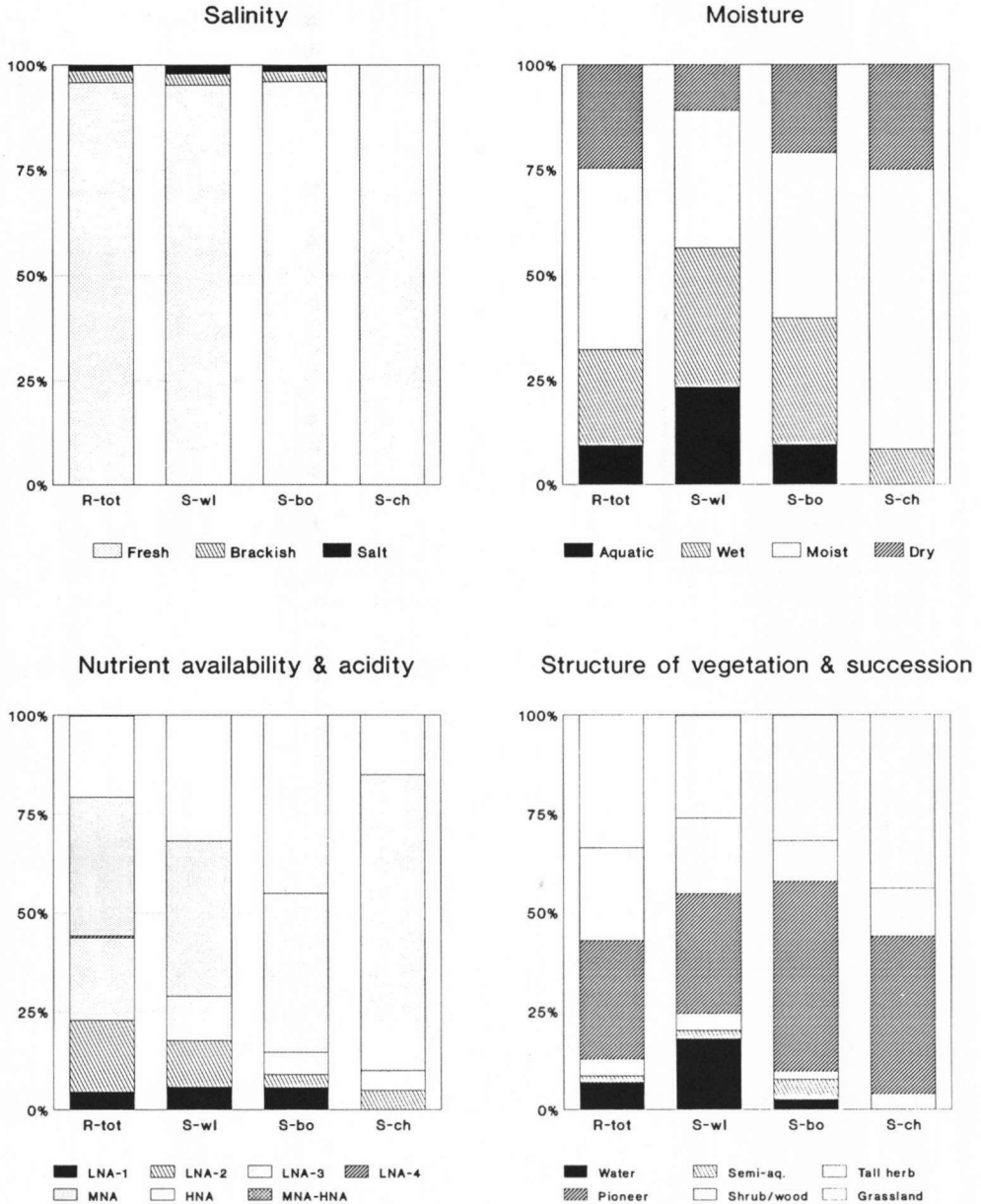


Fig. 5. Comparison of recent taxa with subfossil taxa with regard to the environmental characteristics. Only taxa with small ecological ranges are incorporated. Abbreviations: see Figs 3 and 4.

and belong to grasslands and pioneer vegetations. Taxa that have only been recorded by waterlogged remains resemble the distribution of the recent flora quite well, although plants associated with aquatic habitats are more frequent. Taxa that have been found both by waterlogged and charred remains take up a middle position. However, the high percentage of taxa indicative of high nutrient availability emphasizes that they represent a separate group of plants.

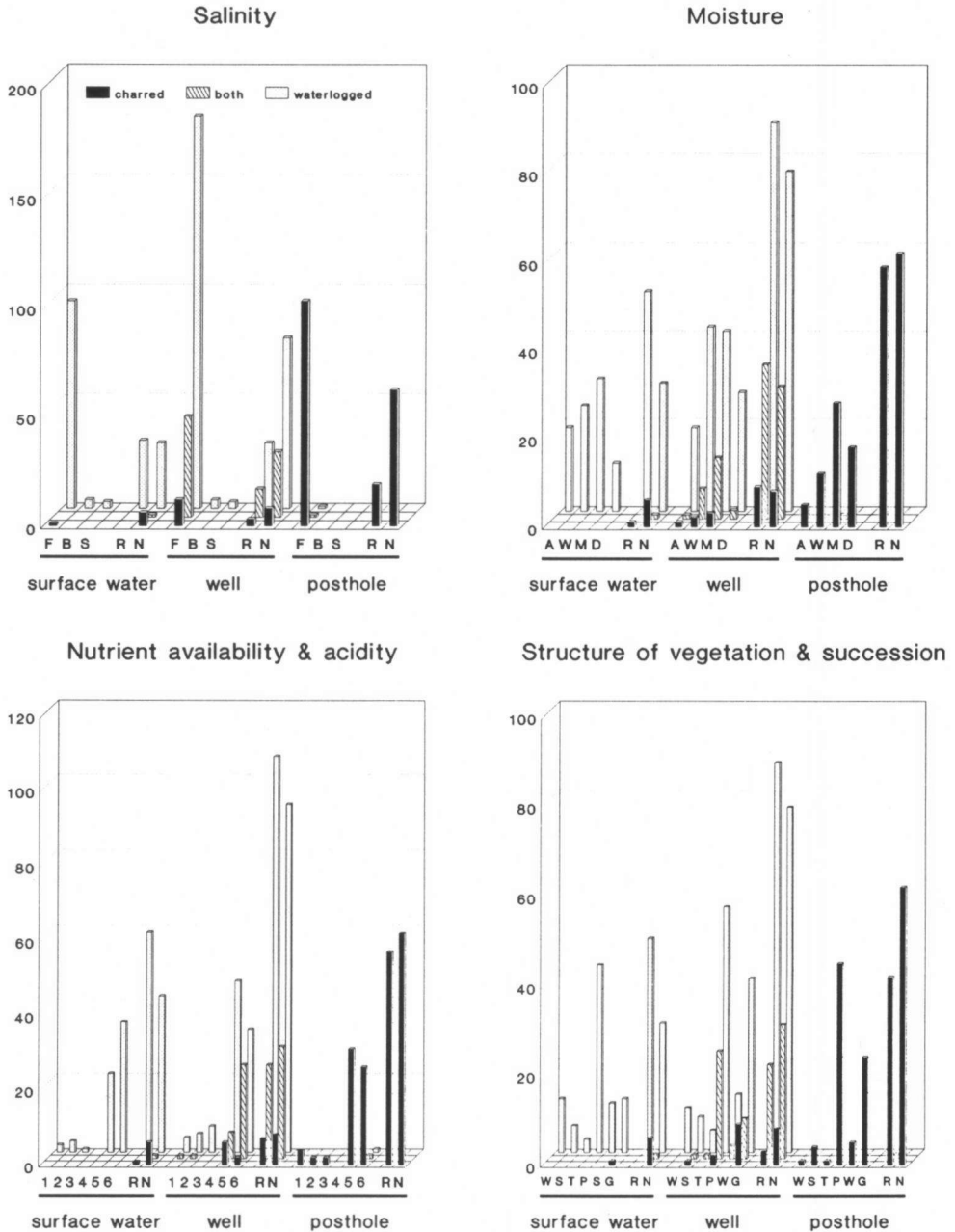


Fig. 6. Representation of the environmental characteristics by subfossil taxa with respect to the different types of preservation and three different feature types. Taxa with a broad ecological range (R) or those that are not coded (N) are only considered with reference to the type of preservation. For each characteristic, the different categories correspond with those of Fig. 5 and are put in the same order.

To illustrate the influence of feature types on distribution patterns, taxa dating from the Roman Period and the Middle Ages and originating from surface water (canals, creeks and rivers), wells and postholes were analysed in connection with the type of

preservation (Fig. 6). Sediments of surface water predominantly yield waterlogged remains, whereas in postholes almost without exception charred remains are found. Wells are well known for the dumping of household rubbish and, together with wet conditions that prevent organic decay, they deliver both waterlogged and charred plant remains. Because these samples are smaller, the categorization with respect to the type of presentation (only waterlogged, only charred or both waterlogged and charred) differs from that of the complete subfossil record and consequently also shows a shift in the distribution with respect to the four environmental categories. For example, the percentage of taxa indicative of high nutrient availability in proportion to that of taxa indicative of moderate nutrient availability is low when all charred subfossil records are involved (Fig. 5: S-ch), while they are almost equal when only charred taxa from postholes are considered (Fig. 6: posthole nos. 5 and 6). Thus, other features rich in charred remains will be characterized by taxa indicative of moderate nutrient availability.

Figure 7 shows how the distribution of the different characteristics of each environmental category is affected by species frequency in the records. Because arable weeds especially will be biased in favour of partial analyses (preliminary reports), the frequencies of subfossil taxa refer to the number of sites from which more than 25 taxa were recorded: Sub-r: 1–5; Sub-m: 6–25; Sub-f: >26 (maximum value: 76). Consequently, the distribution pattern of these subfossil taxa will approximately match the dots representing the two largest groups in Fig. 1. To strengthen the effect of frequency, the recent taxa were reduced to those taxa not mentioned in the subfossil record. For this sample of recent taxa, the distribution over three frequency classes is based on the atlas-square-frequency (ASF): Rec-r: 1–3; Rec-m: 4–6; Rec-f: 7–9. The six groups were put in such an order that the most frequently recorded subfossil and recent taxa were placed at the outermost right and left sides, while the rarest subfossil and recent taxa were placed next to each other in the middle of the diagrams. From this sequence it is clear that the distribution of the different categories of each environmental characteristic is highly biased by the frequency. Taxa frequently mentioned in the subfossil record are particularly indicative of environments with fresh water and wet to moist soils with a high nutrient supply and belong to pioneer vegetations. On the other hand, taxa that are very common but have not yet been recorded on the basis of subfossil remains represent a greater variety of environmental characteristics. Conspicuous differences are shown in the distribution patterns with respect to each of the four environmental categories. Saline and brackish plants are well represented by frequent subfossil and rare recent taxa and therefore match each other in a reverse order (Fig. 7: salinity). With respect to the moisture regime, the increase of dry conditions at the expense of wet conditions characterized by subfossil taxa in order of frequent to rare, is strengthened by the recent taxa (Fig. 7: moisture). Although represented by a different proportion, both frequent subfossil and recent taxa are more indicative of habitats with a high nutrient supply than are rare taxa. In particular, rare recent taxa distinguish themselves from others by the high percentage of basic, low nutrient supply (Fig. 7: nutrient availability and acidity, LNA-3). The shift in the distribution pattern with respect to the structure of the vegetation and stage of succession resembles the moisture regime. The proportion of pioneer plants has changed in favour of plants growing in shrubs and woodlands. Moreover, frequently recorded subfossil plants do not represent water vegetation as all other groups do (Fig. 7: structure of vegetation and succession).

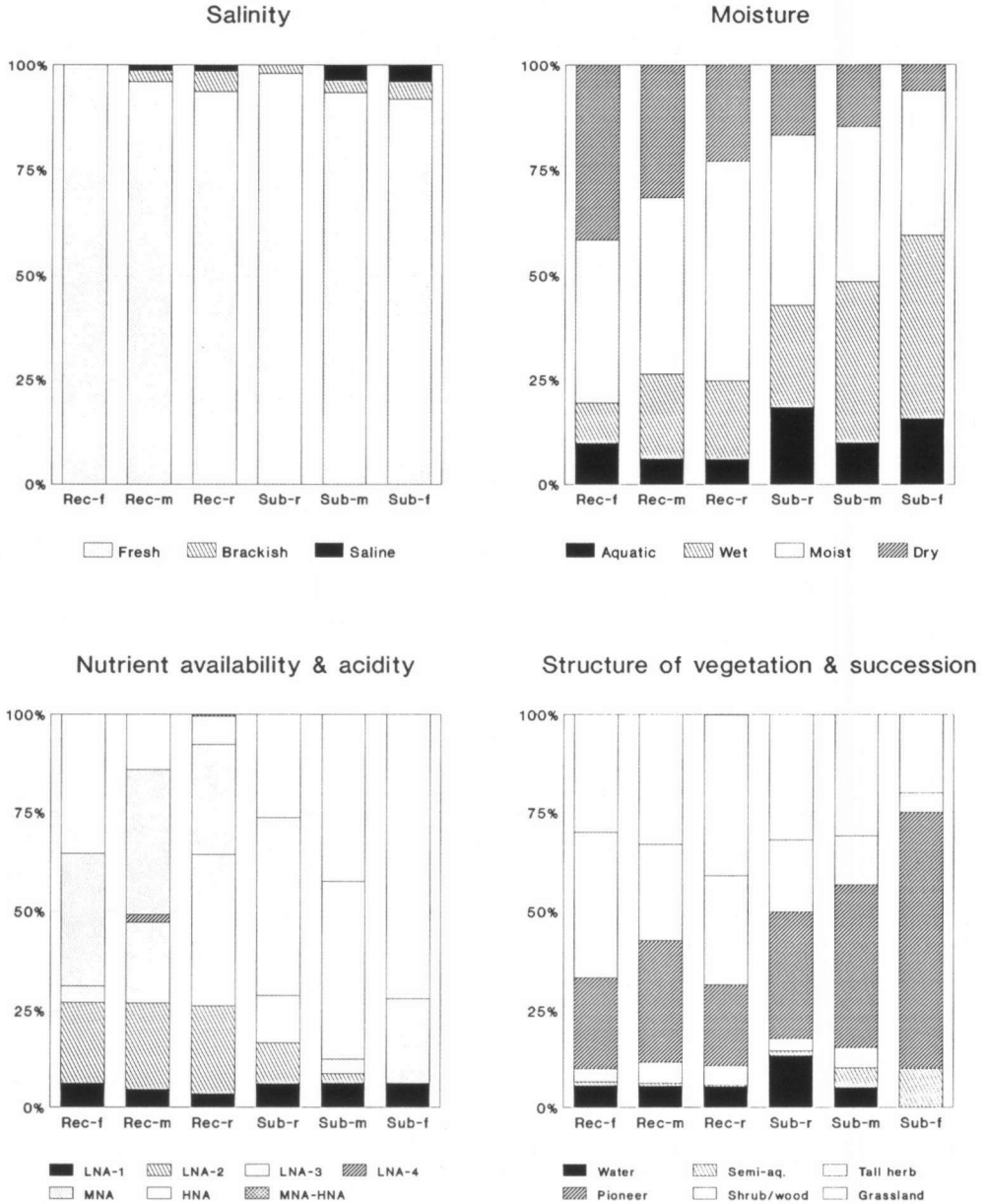


Fig. 7. Comparison of recent taxa with subfossil taxa with regard to the (a)biotic characteristics. Only taxa with small ecological ranges are incorporated while recent taxa are restricted to those being no part of the subfossil record. Both recent (Rec) and subfossil (Sub) taxa are presented in three frequency classes: frequent (f), medium (m) and rare (r). For further restriction: see text. Other abbreviations: see Figs 3 and 4.

Indicator plants

Some classes in the CML-classification have been omitted or merged. Species indicative of saline and brackish environments were classified under halophytes. The groups of

Table 1. Indicator taxa for salinity. Weights are presented separately for waterlogged (WL) and charred (CH) remains

WL	CH	Indicator taxa
Halophytic		
12	5	<i>Althaea officinalis</i>
3	16	<i>Apium graveolens</i>
5	—	<i>Armeria maritima</i>
3	95	<i>Aster tripolium</i>
101	—	<i>Carex distans</i>
491	—	<i>Cochlearia officinalis</i>
4	2	<i>Glaux maritima</i>
1	3	<i>Juncus gerardi</i>
6	—	<i>Limonium vulgare</i>
5	—	<i>Oenanthe lachenalii</i>
58	—	<i>Parapholis strigosa</i>
5	4	<i>Plantago maritima</i>
4	4	<i>Puccinellia distans</i>
11	—	<i>Puccinellia maritima</i>
20	—	<i>Ruppia maritima</i>
2	47	<i>Salicornia europaea</i> s.l.
2	1	<i>Scirpus lacustris</i> ssp. <i>tab.</i>
3	8	<i>Spergularia maritima</i> /salina
3	42	<i>Suaeda maritima</i>
1	4	<i>Triglochin maritima</i>
Glycophytic		
5	14	<i>Alnus glutinosa</i>
3	12	<i>Anagallis arvensis</i>
3	104	<i>Berula erecta</i>
2	1	<i>Bromus hordeaceus</i> /secalinus
2	20	<i>Carex rostrata</i> /vesicaria
3	3	<i>Cladium mariscus</i>
1	3	<i>Erica tetralix</i>
3	—	<i>Eupatorium cannabinum</i>
5	4	<i>Galium aparine</i>
3	8	<i>Galium palustre</i>
4	9	<i>Glyceria fluitans</i>
2	144	<i>Hydrocotyle vulgaris</i>
1	6	<i>Lycopus europaeus</i>
2	37	<i>Lythrum salicaria</i>
2	1	<i>Polygonum convolvulus</i>
2	21	<i>Ranunculus repens</i>
3	—	<i>Solanum dulcamara</i>
4	60	<i>Stachys palustris</i>
2	1149	<i>Typha angustifolia</i> /latifolia
1	10	<i>Urtica dioica</i>

plants indicative of soils with low nutrient availability were merged, thus leaving the difference in acidity aside. Plants that are indicative of the transitional stage of medium to high nutrient availability were omitted, for they are per definition characterized by a broad ecological range and, furthermore, were not represented by the subfossil record. With respect to the structure of vegetation and stage of succession plants indicative of

Table 2. Indicator taxa for moisture regime. Weights are presented separately for waterlogged (WL) and charred (CH) remains

WL	CH	Indicator taxa
Aquatic habitats		
1	7	<i>Alisma plantago-aquatica</i>
124	3	<i>Ceratophyllum submersum</i>
8	—	<i>Cicuta virosa</i>
5	30	<i>Hippuris vulgaris</i>
2	16	<i>Menyanthes trifoliata</i>
11	—	<i>Myriophyllum spicatum</i>
68	—	<i>Najas marina</i>
14	—	<i>Nuphar lutea</i>
5	—	<i>Nymphaea alba</i>
3	329	<i>Oenanthe aquatica</i>
9	—	<i>Potamogeton natans</i>
22	—	<i>Potamogeton pectinatus</i>
43	—	<i>Potamogeton polygonifolius</i>
10	329	<i>Potentilla palustris</i>
43	—	<i>Ranunculus lingua</i>
4	110	<i>Rumex hydrolapathum</i>
14	—	<i>Ruppia maritima</i>
1	1	<i>Scirpus lacustris</i>
4	10	<i>Sparganium erectum</i>
4	—	<i>Zannichellia palustris</i>
Wet habitats		
3	19	<i>Alopecurus geniculatus</i>
3	53	<i>Aster tripolium</i>
3	7	<i>Carex flavallepido carpaloederi</i>
13	212	<i>Filipendula ulmaria</i>
4	2	<i>Galium palustre</i>
4	1	<i>Glaux maritima</i>
2	27	<i>Hydrocotyle vulgaris</i>
7	—	<i>Juncus effusus</i>
1	2	<i>Juncus gerardi</i>
4	16	<i>Myrica gale</i>
5	2	<i>Plantago maritima</i>
2	1	<i>Ranunculus flammula</i>
24	21	<i>Scirpus sylvaticus</i>
16	—	<i>Scutellaria galericulata</i>
3	4	<i>Spergularia maritima salina</i>
7	2	<i>Stellaria aquatica</i>
9	—	<i>Thalictrum flavum</i>
5	—	<i>Thelypteris palustris</i>
18	—	<i>Triglochin palustris</i>
12	212	<i>Valeriana officinalis</i>

Continued

tall herb vegetations were omitted, because the number of plants is low both in the recent flora and in the subfossil record, making it unfeasible to select a sufficient number of indicator species.

As a result, 14 groups of indicator plants were compiled, all except one consisting of 20 taxa (Tables 1–4). The combination of the above-mentioned criteria resulted

Table 2. *Continued*

WL	CH	Indicator taxa
Moist habitats		
3	4	<i>Agrostemma githago</i>
5	1379	<i>Anthemis cotula</i>
6	17	<i>Atriplex littoralis/prostrata</i>
1	2	<i>Atriplex patula/prostrata</i>
9	1379	<i>Cerastium fontanum</i>
8	197	<i>Conium maculatum</i>
9	27	<i>Euphorbia helioscopia</i>
7	7	<i>Lapsana communis</i>
5	5	<i>Matricaria maritima</i>
1	2	<i>Polygonum aviculare</i>
1	1	<i>Polygonum lapathifolium</i>
2	2	<i>Polygonum persicaria</i>
4	20	<i>Prunella vulgaris</i>
2	36	<i>Ranunculus sardous</i>
5	3	<i>Rumex crispus</i>
10	44	<i>Rumex obtusifolius</i>
5	5	<i>Sinapis arvensis</i>
2	13	<i>Sonchus asper</i>
5	14	<i>Sonchus oleraceus</i>
7	77	<i>Thlaspi arvense</i>
Dry habitats		
6	120	<i>Anthemis arvensis</i>
29	8	<i>Apera spica-venti</i>
3	77	<i>Arnoseris minima</i>
2	154	<i>Centaurea cyanus</i>
16	1076	<i>Descurainia sophia</i>
10	179	<i>Galeopsis segetum</i>
8	35	<i>Hyoscyamus niger</i>
7	108	<i>Hypochaeris glabra/radicata</i>
15	—	<i>Juniperus communis</i>
13	538	<i>Moehringia trinervia</i>
18	—	<i>Nepta cataria</i>
13	—	<i>Papaver argemone</i>
20	—	<i>Pteridium aquilinum</i>
12	538	<i>Reseda luteola</i>
1	1	<i>Rumex acetosella</i>
2	10	<i>Scleranthus annuus</i>
10	28	<i>Setaria pumila</i>
2	1	<i>Spergula arvensis</i>
423	—	<i>Veronica hederifolia</i>
29	15	<i>Vicia hirsuta</i>

in a selection of 188 taxa, one of them accepted on both species and subspecies level (*Scirpus lacustris* s.l. and *Scirpus lacustris* ssp. *tabernaemontani*) and some others as a combination of species (for example: *Atriplex patula/prostrata* and *Carex rostrata/vesicaria*).

Table 3. Indicator taxa for nutrient availability. Weights are presented separately for waterlogged (WL) and charred (CH) remains

WL	CH	Indicator taxa
Soils with low nutrient availability		
1	1	<i>Calluna vulgaris</i>
12	424	<i>Descurainia sophia</i>
11	4	<i>Empetrum nigrum</i>
1	1	<i>Erica tetralix</i>
3	28	<i>Eriophorum vaginatum</i>
6	14	<i>Hyoscyamus niger</i>
6	—	<i>Juncus squarrosus</i>
11	—	<i>Juniperus communis</i>
15	—	<i>Linum catharticum</i>
9	212	<i>Moehringia trinervia</i>
5	106	<i>Molina caerulea</i>
3	33	<i>Myrica gale</i>
7	—	<i>Oxycoccus palustris</i>
7	71	<i>Pedicularis palustris</i>
4	14	<i>Potentilla erecta</i>
15	—	<i>Pteridium aquilinum</i>
9	212	<i>Reseda luteola</i>
7	—	<i>Rhynchospora alba</i>
15	42	<i>Scirpus setaceus</i>
4	85	<i>Vaccinium myrtillus</i>
Soils with moderate nutrient availability		
1	3	<i>Agrostemma githago</i>
3	941	<i>Anthemis cotula</i>
3	67	<i>Arnoseris minima</i>
2	6	<i>Carex cuprinalvulpina</i>
2	10	<i>Carex disticha</i>
4	314	<i>Carex paniculata</i>
3	36	<i>Carex pseudocyperus</i>
2	134	<i>Centaurea cyanus</i>
4	134	<i>Conium maculatum</i>
4	86	<i>Hippuris vulgaris</i>
1	67	<i>Lychnis flos-cuculi</i>
6	3	<i>Medicago lupulina</i>
3	941	<i>Oenanthe aquatica</i>
15	2	<i>Plantago lanceolata</i>
7	235	<i>Polygonum minus</i>
2	14	<i>Prunella vulgaris</i>
2	8	<i>Raphanus raphanistrum</i>
2	9	<i>Scleranthus annuus</i>
1	1	<i>Spergula arvensis</i>
7	86	<i>Stellaria graminea</i>

Continued

DISCUSSION

Species frequency and preservation

Leaving out cereals, oil and fibre crops, and plants identified on the level of genus and family, the most frequently recorded taxa arranged in decreasing order are:

Table 3. *Continued*

WL	CH	Indicator taxa
Soils with high nutrient availability		
5	168	<i>Alopecurus geniculatus</i>
1	2	<i>Atriplex patula/prostrata</i>
3	32	<i>Capsella bursa-pastoris</i>
1	1	<i>Chenopodium album</i>
2	4	<i>Chenopodium ficifolium</i>
11	142	<i>Cirsium arvense</i>
5	3	<i>Echinochloa crus-galli</i>
7	14	<i>Glyceria fluitans</i>
8	116	<i>Glyceria maxima</i>
5	6	<i>Matricaria maritima</i>
15	206	<i>Phalaris arundinacea</i>
4	8	<i>Poa annua</i>
2	49	<i>Ranunculus sardous</i>
5	4	<i>Rumex crispus</i>
3	8	<i>Scirpus maritimus</i>
2	7	<i>Solanum nigrum</i>
6	19	<i>Sonchus arvensis</i>
6	97	<i>Stachys palustris</i>
1	3	<i>Stellaria media</i>
2	42	<i>Urtica urens</i>

Chenopodium album, *Stellaria media*, *Polygonum aviculare*, *Polygonum lapathifolium*, *Eleocharis palustris*, *Urtica dioica*, *Atriplex patula/prostrata*, *Polygonum convolvulus*, *Plantago major*, *Polygonum persicaria*, *Juncus bufonius*, *Sonchus asper*, *Juncus gerardi*, *Corylus avellana*, *Rumex acetosella* and *Lycopus europaeus*. Because plants from all sites were taken into account, this sequence is partly determined by the analyses of samples that were selected for their crop remains. The strong representation of ruderals and arable weeds can be explained by their life strategies. The huge number of seeds that are produced are for the most part dispersed over only short distances. Many seeds are dispersed in time which is favoured by persistent seed banks and seed longevity. Even after germination, seed coats of many of the above-mentioned species may be retained and become part of the subfossil record. Some arable weeds frequently mentioned by subfossil records are now quite rare or even seriously endangered: *Arnoseria minima* (atlas-square-frequency, ASF: 15), *Bromus secalinus* (ASF: 18) and *Agrostemma githago* (ASF: 31) (Weeda *et al.* 1990).

Many species have not been recorded by subfossil remains for The Netherlands until now. Many reasons can be given for this absence, including rarity of species, vegetative propagation, poor or no seed set, chemistry of the fruit and/or seed coat and unfavourable conditions for preservation, e.g. *Artemisia maritima* has never been recorded although today it is a common species of salt-marshes. Its absence can be explained by its very late flowering, resulting in an unstable seed set. Seeds found in drift litter (Cappers 1993) were partly unripe, partly germinating so that the fragile seed coat was destroyed, and partly affected by predation; these factors combined mean it is most unlikely to be preserved.

Table 4. Indicator taxa for structure of the vegetation and stage of succession. Weights are presented separately for waterlogged (WL) and charred (CH) remains

WL	CH	Indicator taxa
Water vegetation		
6	—	<i>Ceratophyllum demersum</i>
46	1	<i>Ceratophyllum submersum</i>
2	9	<i>Hippuris vulgaris</i>
4	—	<i>Myriophyllum spicatum</i>
11	—	<i>Myriophyllum verticillatum</i>
25	—	<i>Najas marina</i>
5	—	<i>Nuphar lutea</i>
2	—	<i>Nymphaea alba</i>
11	—	<i>Nymphoides peltata</i>
11	—	<i>Potamogeton alpinus</i>
5	—	<i>Potamogeton crispus</i>
3	—	<i>Potamogeton natans</i>
8	—	<i>Potamogeton pectinatus</i>
16	—	<i>Potamogeton polygonifolius</i>
5	—	<i>Potamogeton praelongus</i>
5	—	<i>Potamogeton pusillus</i>
1	—	<i>Ranunculus</i> subg. <i>Batrachium</i>
5	—	<i>Ruppia maritima</i>
6	—	<i>Stratiotes aloides</i>
1	—	<i>Zannichellia palustris</i>
Pioneer vegetation		
5	19	<i>Anagallis arvensis</i>
1	2	<i>Atriplex littoralis/prostrata</i>
6	23	<i>Atriplex patula/prostrata</i>
3	32	<i>Capsella bursa-pastoris</i>
1	1	<i>Chenopodium album</i>
2	4	<i>Chenopodium ficifolium</i>
2	43	<i>Chenopodium glaucum/rubrum</i>
30	36	<i>Chenopodium polyspermum</i>
5	3	<i>Echinochloa crus-galli</i>
1	13	<i>Juncus bufonius</i>
5	6	<i>Matricaria maritima</i>
1	6	<i>Plantago major</i>
4	8	<i>Poa annua</i>
3	16	<i>Raphanus raphanistrum</i>
6	—	<i>Rorippa palustris</i>
2	2	<i>Rumex acetosella</i>
9	—	<i>Sagina apetalaprocombens</i>
2	7	<i>Solanum nigrum</i>
1	3	<i>Stellaria media</i>
2	42	<i>Urtica urens</i>

Continued

In future research, special attention should be drawn to species which are lacking in the subfossil record of The Netherlands, but which could be expected on the basis of the ecological analyses of the subfossil record and the current distribution. They concern plants that are (i) quite common now, not being the result of a recent expansion, and

Table 4. *Continued*

WL	CH	Indicator taxa
Grassland		
3	2	<i>Carex cuprinalvulpina</i>
3	3	<i>Carex disticha</i>
6	292	<i>Cerastium fontanum</i>
1	3	<i>Juncus gerardi</i>
7	7	<i>Knautia arvensis</i>
2	49	<i>Leontodon autumnalis</i>
30	27	<i>Lolium perenne</i>
1	21	<i>Lychnis flos-cuculi</i>
9	1	<i>Medicago lupulina</i>
5	22	<i>Oenanthe fistulosa</i>
6	10	<i>Potentilla erecta</i>
3	4	<i>Prunella vulgaris</i>
4	3	<i>Puccinellia distans</i>
10	19	<i>Ranunculus acris</i>
2	2	<i>Ranunculus flammula</i>
9	27	<i>Stellaria graminea</i>
8	—	<i>Taraxacum officinale</i> s.l.
20	146	<i>Trifolium pratense</i>
5	4	<i>Trifolium repens</i>
18	—	<i>Triglochin palustris</i>
Shrub and woodland		
15	101	<i>Acer campestre</i>
2	9	<i>Alnus glutinosa</i>
3	—	<i>Betula pendula/pubescens</i>
8	—	<i>Castanea sativa</i>
5	—	<i>Cornus sanguinea</i>
1	1	<i>Corylus avellana</i>
16	8	<i>Crataegus monogyna</i>
29	—	<i>Fagus sylvatica</i>
2	804	<i>Humulus lupulus</i>
7	—	<i>Juniperus communis</i>
2	—	<i>Mespilus germanica</i>
6	402	<i>Moehringia trinervia</i>
2	62	<i>Myrica gale</i>
8	—	<i>Pinus sylvestris</i>
8	—	<i>Populus tremula</i>
2	9	<i>Prunus spinosa</i>
8	11	<i>Quercus petraea/robur</i>
2	80	<i>Sambucus nigra</i>
24	54	<i>Stachys sylvatica</i>
22	—	<i>Torilis japonica</i>

Continued

(ii) characterized by one of the two conditions of each characteristic that is highly represented by plants that are frequently mentioned in the subfossil record (Fig. 7: fresh or brackish, wet–moist, moderate–high nutrient availability, and pioneer or grassland plants). Most of these species are already known from other countries, e.g. *Cardamine pratensis*, *Geranium molle*, *Euphorbia esula*, *Heracleum sphondylium*, *Symphytum*

Table 4. *Continued*

WL	CH	Indicator taxa
Semi-aquatic helophytic habitats		
1	7	<i>Alisma plantago-aquatica</i>
87	—	<i>Carex lasiocarpa</i>
8	—	<i>Cicuta virosa</i>
2	16	<i>Menyanthes trifoliata</i>
10	329	<i>Potentilla palustris</i>
43	—	<i>Ranunculus lingua</i>
4	110	<i>Rumex hydrolapathum</i>
1	1	<i>Scirpus lacustris</i>
84	—	<i>Sparganium emersum</i>
4	10	<i>Sparganium erectum</i>

officinale, *Crepis biennis*, *Holcus mollis*, *Dactylus glomerata* and *Alopecurus myosuroides* (Goodwin 1975; Jensen 1987; Körber-Grohne 1990; Willerding 1986).

Ecological characterization on the basis of the total subfossil record

For a well-considered interpretation of indicator values related with subfossil records, it is important to have a frame of reference. Thus far, the interpretation of indicator values, usually presented in so called eco-diagrams (e.g. Brinkkemper 1993; Van Zeist 1986), has been restricted to a comparison of subfossil records from different samples or sites with each other and may apply to differences with respect to feature types, locations and periods. A main disadvantage of this approach concerns the selective representation of the subfossil record. The analysis of the Holocene subfossil record of The Netherlands shows that only 36% of the recent flora has been attested until now and that the representativeness of this sample with respect to environmental characteristics is biased by the type of preservation, species frequency and archaeological context. Especially on a high level of comparison, such as sites or main periods, this may seriously influence the diagnostic value of eco-diagrams. If all plants recovered are taken into account, a more reliable interpretation of the environmental characteristics may be obtained by a comparison of samples on a low level; for example, from different periods within a site, both with each other and with the total (subfossil) flora.

The ecological characterization of the subfossil record in this study is limited by the exclusion of records based only on pollen and wood identifications. Although the characterization is in concordance with data sets restricted to the same type of remains, it is emphasized that a correction of this picture may be obtained by including these records. For example, woody plants such as *Acer*, *Fraxinus* and *Ulmus* will be underestimated, while others, such as *Tilia*, are completely absent although they are recorded by both pollen and wood identifications (e.g. Casparie 1990).

In principle, all wild plant species are eligible for the analyses of the environment. Although assemblages are highly biased by the type of preservation and the related archaeological context, this is also true of specimens represented by charred remains. Found in connection with cultivated plants, they will often represent plant communities from man-made landscapes. On the other hand, charring caused by man, such as the burning of rubbish, may also affect specimens from more natural environments. Natural processes may also be responsible for plant remains becoming charred.

Besides lightning, salt spray should also be considered in this respect. Plants that grow near the sea and are exposed to sea spray may show a characteristic pattern of black spots on the tissue (Cappers, personal observation).

The use of indicator values based on recent studies for the interpretation of the Holocene subfossil record, assumes the persistence of those values through time. In this context it should be realized that ecological ranges are often much smaller than physiological ones. The composition of a specific plant community is determined by environmental characteristics, the capability of occupying available safe sites (by seed bank and seed rain) and competitive ability of species. Therefore, it is justifiable to assume that the composition of plant communities has changed in the course of the Holocene, while the ecological requirements could have been quite stable. Taking the line that fossil assemblages not matching current plant communities have to be interpreted as originating from a single plant community, the explanation is mostly directed to changing environmental conditions (e.g. Van der Veen 1992) rather than to a shift in the ecological requirement of the species themselves (e.g. Lange 1990). Although unspecialized species are unsuitable for the reconstruction of environmental conditions, they are of special interest for they may sustain environmental changes quite well and will be less endangered than species that have become specialists.

Use of indicator plants

Instead of using all recovered plants, it is also possible to build up an overall picture of the environmental conditions by the use of a selected number of indicator plants. In comparison with the selection of halophytes and glycophytes made by Behre (1991) the number of plants is enlarged and, especially with respect to the glycophytes, some other plants have been chosen. This is mainly the result of different criteria that were used (see Introduction and Results). *Centaurium pulchellum* and *Hippuris vulgaris* were substituted for they are indicative of both brackish and fresh water. While Behre links salinity to grasslands, the groups presented in this study are deliberately compiled by taxa that are indicative of the characteristics concerned and at the same time are as unspecialized as possible with respect to the other characteristics.

The use of a selected number of plants increases the problem of representation and with that the need for a well-considered quantitative approach. To meet this objection, in addition to the sample frequency introduced by Brinkkemper (1993), a taxon weight is assigned to all taxa. For practical reasons, these weights are based on the sample frequency of the Holocene subfossil records and, in fact, these have to be considered as the derivative of parameters such as seed production, dispersal strategies, seed longevity and dormancy types. Until now, more or less standardized data with respect to these parameters have not been available.

The use of taxon weights enables one to deal with the different chances of species recovery. Taphonomic processes as well as sampling and recovery methods determine the composition of the subfossil record. Comparable to the species–area curves used in vegetation description and showing the relationship between the number of species and the size of the sampling, are the species–volume curves used in seed bank analyses and palaeobotanical studies and displaying in a similar way the number of species depending on the volume examined (Hutchings 1986; Dick 1989). Lange (1990) presented an analogous correlation by plotting the relationship between the number of seeds and the number of species per sample. Although plants that are considered to be rare may be detected in the very first part of the first sample being examined, it is more likely that

they become part of the record only when a considerable volume of a number of samples has been looked through. Therefore, it is justifiable to multiply the presence/absence scores with the taxon weight, representing the chance of being recovered. To adjust the presence/absence scores for the uneven representation of samples per unit of analyses, they are divided by the sample frequency. Thus, for a unit of samples the indicator value (I_u) of environmental characteristic j is calculated as:

$$I_u = \sum_{i=1}^{m_j} \left(\frac{M_i}{M_j} \right) \cdot W_i \quad (3)$$

where M_i is the number of samples with taxon i , M_j is the number of samples within the unit of analyses, and W_i is the character weight of taxon i .

The maximum number of indicator taxa (m_j) for each environmental characteristic depends on the actual number of taxa that is present in the subfossil record. From Tables 1–4 it is clear that ranges in taxon weights differ between the groups of indicator taxa that are distinguished. Consequently, the maximum value of I_u varies with the environmental characteristic. Therefore, it is emphasized that the presentation of individual indicator values for a specific environmental factor as a ratio (e.g. halophytes/glycophytes) has to be avoided. Especially when there are more than two groups of indicator taxa, which is the case for moisture regime, nutrient availability and the structure of vegetation, the interpretation of the diagram will become obscure. Moreover, a ratio tends to the interpretation of shifts in terms of species competition for space. Although this may be true, it is also possible that, for example, the increase of glycophytes is the result of natural succession or changes in the vegetation due to human activity in the same area.

Because the ecological groups that were used to characterize the palaeobotanical record are grafted on data from The Netherlands, prudence is called for in the use of these classifications in connection with data from other countries. Analyses of relevant palaeobotanical data must reveal to what extent the selection of indicator taxa and their weights as a derivative of the frequency have to be adapted to areas other than The Netherlands. On the other hand, the availability of databases from neighbouring countries can be used to improve the selection of indicator taxa because it enlarges especially information on preservation and, in connection with this, the chance of recovery. Taxa that are somewhat problematic with respect to their indicator value (such as *Conium maculatum* as indicative of soils with moderate nutrient availability) but that were selected because the combination of the criteria used (see Materials and Methods) left no choice, could be exchanged for less debatable ones.

To demonstrate the effect of different approaches to the use of indicator plants, the subfossil record of medieval Leeuwarden was analysed with respect to salinity (Van Zeist *et al.* 1987; Fig. 8). Although Leeuwarden is now situated inland, in former times it was located along a sea arm, the Middle Sea. Salt-marshes were present in the area in the early stages of the habitation. To protect themselves against floods, the inhabitants started with the embankment of the Middle Sea, which would have been completed by 1100. About 180 years later, a dike in the Middle Sea north of Leeuwarden was constructed, reducing further the influence of the sea (Van Zeist *et al.* 1987). Figure 8A and B are constructed on the basis of the indicator taxa presented by Behre (1991) while for Fig. 8C the indicator taxa from this study are used. Figure 8A and B are very much alike and differ only with respect to periods that comprise a reasonable amount of

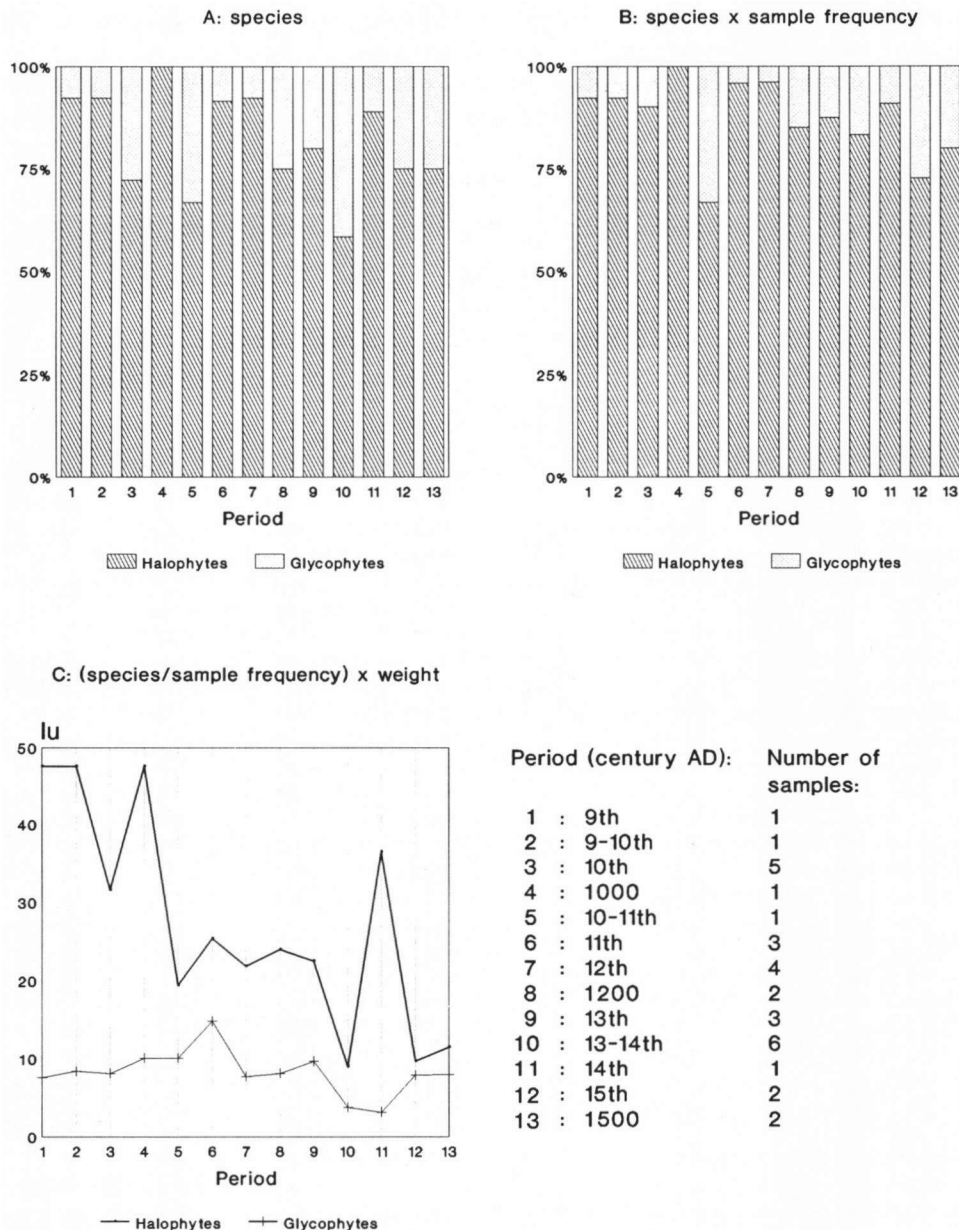


Fig. 8. Fluctuations of indicator plants for salinity from medieval Leeuwarden: A and B are based on indicator plants presented by Behre; C is based on the indicator plants from Table 1. In Fig. 8A the presence ratio is calculated, in Fig. 8B the frequency ratio and in Fig. 8C the indicator value I_u .

samples. A decrease of halophytes is only clearly shown in Fig. 8C. Furthermore, this last figure also shows that glycophytes are more or less equally represented over the whole period considered. The decline of halophytes in the tenth century can be explained by the different composition of the five samples, while the strong increase in the fourteenth century is partly influenced by the presence of indicator plants with relatively high

weight characters when compared with those of the eleventh and twelfth centuries. So the selection of indicator plants, a correction for the chance of recovery, the way in which the number of samples is taken into account and the presentation of separate curves will strongly improve the interpretation of environmental changes.

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APPENDIX 1

Publications from which subfossils records are used for the analyses.

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