Patterns and processes in natural wetland vegetation in the Dutch fluvial area: a palaeoecological study

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SUMMARY

Palynological study of deposits in the residual channel and flood basin of a former Rhine distributary reveals the species composition and development of natural wetland vegetation prior to major human interference. Flood-basin vegetation resembled a Typho-Phragmitetum thelypteridetosum vegetation during river activity. After this, vegetation succession shows a terrestrialization pattern, although duration of terrestrialization phases suggests continuous rising water levels in the flood basin. Grazing of wetland mammals is suggested by a sample probably representing a fossil excrement. During minor river activity reed marshes were present along the margins of the active channel, with Typha angustifolia and Sparganium in the deeper parts. After river activity ended a Bidentetea-vegetation originated on the lower clayey parts of the natural levees, succeeded by an extension of reed marshes. There are traces of fire, which temporarily disturbed the vegetation. Vegetation succession ended with the development of alder carr.

Key-words: fluvial area, natural wetland vegetation, nature development, palynology.

INTRODUCTION

Nature conservation in The Netherlands is increasingly engaged in transforming agricultural lands into new nature areas by nature development (Baerselman & Vera 1989; Gabor 1990). Crucial in this approach is the construction of 'ecological references' to identify natural ecosystem processes. Palynological research can contribute to such references by revealing vegetation patterns and dynamics of fluvial areas prior to human interference (De Klerk *et al.* 1997).

In this paper patterns and processes in wetland vegetation of a fossil river system are reconstructed for the period 3500–2000 year BP.

METHODS

Sample collection and preparation and results of AMS dating are described by De Klerk et al. (1997).

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Pollen and spores were identified by reference to Moore et al. (1991), Faegri & Iversen (1989), the Northwest European Pollen Flora (Punt 1976; Punt & Clarke 1980, 1981, 1984; Punt et al. 1988; Punt & Blackmore 1991, Punt et al. 1995), Van Geel (1978), Van Geel et al. (1981), Van Geel et al. (1986) and Van der Wiel (1982).

The pollen diagrams were drawn with the programs TILIA 1.12 and TILIA GRAPH 1.18 (Grimm 1992). Pollen percentage values are expressed as percentages of the sum of pollen types supposedly originating from upland plants, using a pollen sum of approximately 200 pollen grains. All pollen and spores were given the suffix '-type' or '-group' to stress that these objects are morphological, not taxonomical entities. If more Dutch taxa are known to produce the same morphological type these taxa are mentioned in the discussion, because these taxa will be the most probable producers of the sporomorphs encountered.

RESULTS AND DISCUSSION

Lithology of the sections

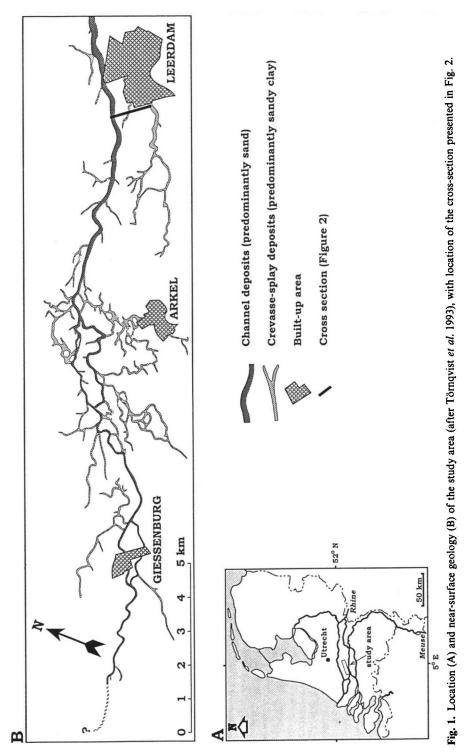
Two sections are discussed in this paper: the residual channel (Oosterwijk I) and the flood basin (Oosterwijk III) of the Schaik alluvial ridge near Leerdam (Figs 1 and 2). The residual channel section contains a lower clay layer, deposited during river activity and a peat layer resulting from subsequent terrestrialization. A similar stratigraphy can be observed in the flood basin section.

River activity in the residual channel, however, was not synchronous with river activity in the flood basin (De Klerk *et al.* 1997). Furthermore, the flood basin section is not continuous, due to a sedimentary hiatus (Törnqvist & Van Dijk 1993).

Regional wetland vegetation

In order to reconstruct local wetland vegetation patterns and developments, local values of wetland pollen types have to be distinguished from the regional background values of the same types. Similar (and often similary low) values of a pollen type in synchroneous parts of two (or more) adjacent cores indicate the regional origin of this type (Janssen 1973).

The wetland diagrams of section Oosterwijk I (Fig. 3) and Oosterwijk III (Fig. 4) show an almost continuous presence of pollen types of open water species, including Nymphaea alba-, Nuphar lutea-, Stratiotes aloides-, Myriophyllum verticillatum- and M. spicatum-type, indicating continuous presence of open water. The low values, however, point to regional values of these pollen types, resulting from the enormous extent of wetlands in this region. Also Polypodiales type spores and pollen of Asteraceae tubuliflorae undiff.-, Asteraceae liguliflorae undiff.- and Rumex acetosa-type (including all Rumex sp.) are continuously present without a distinct stratigraphic pattern. Some intact Thelypteris palustris-type spores make it plausible that the Polypodiales-type spores must be attributed mainly to Thelypteris palustris. The presence of Diporothecatype spores, attributed to a fungus probably parasitizing on Thelypteris (Van Geel et al. 1986), might confirm this assumption, although an unambigous relationship between both taxa is doubtful (B. van Geel, personal communication, 1995). Equal low values for Polypodiales-type spores in both diagrams (except for zone OOS-III-a) indicate that T. palustris was probably not locally present on either site. The constant (high) values of Alnus- and Salix-type pollen point at the continuous presence of alder and willow carr



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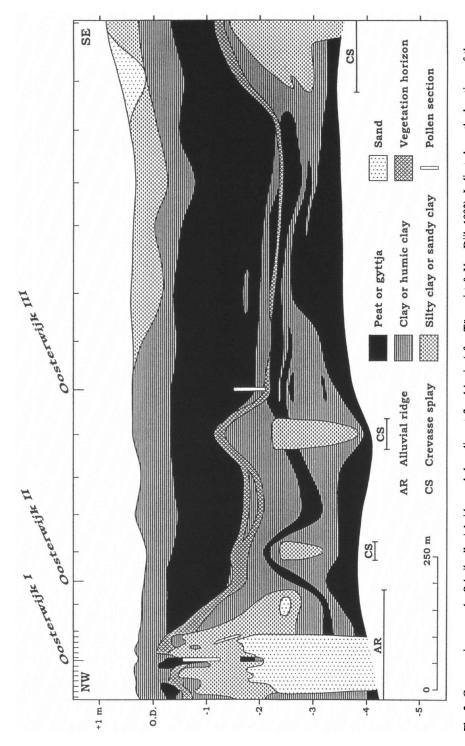


Fig. 2. Cross section over the Schaik alluvial ridge and the adjacent flood basin (after Törnqvist & Van Dijk 1993). Indicated are the locations of the cores Oosterwijk I-III and the pollen sections studied.

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in the area. Alnus-type pollen values of the Oosterwijk I section (Fig. 3) do not exceed the lowest values of the Oosterwijk III section (Fig. 4). This suggests that these values in the residual channel section only reflect regional or extra-local pollen deposition. The presence of an Alnus catkin at a depth of 126 cm (used for ¹⁴C-dating, De Klerk et al. 1997), however, indicates local presence of some Alnus trees. Therefore it is concluded that Alnus was present at the residual channel margins near the sampling site, but not in large amounts.

Vegetation development in the residual channel

The following local wetland pollen zones can be distinguished in the residual channel section (Oosterwijk I, Fig. 3).

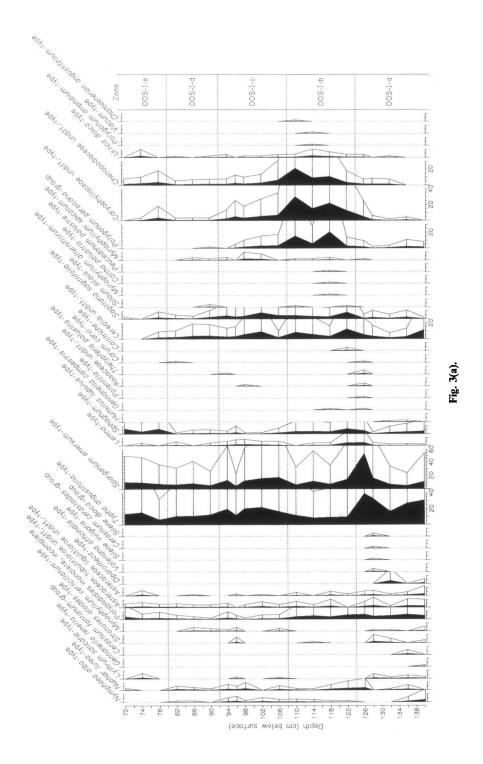
Zone OOS-I-a (140–124 cm), corresponding with the clay layer deposited during minor river activity, is characterized by relative high values of pollen of *Typha angustifolia*-type and (at a depth of 126 cm) an occasional peak of *Sparganium emersum*-type (including all north-western European *Sparganium* sp.). The relatively low values of Poaceae undiff.-type and Cyperaceae undiff.-type pollen may yet reflect extralocal values, as is shown from comparison with the Oosterwijk III diagram, where these pollen types occur with even lower values. This pollen assemblage indicates the presence of semi-aquatic, early terrestrializing vegetation dominated by tall helophytes (Den Held *et al.* 1992). The assemblage points to the presence of *T. angustifolia* and occasional *Sparganium* in the deeper part of the active channel (i.e. at the sample point) and reed marshes closer to the upland.

Zone OOS-I-b (124-108 cm) is characterized by high pollen values of Caryophyllaceae undiff.-type, Polygonum persicaria-group and Chenopodiaceae undiff.-type, indicating the presence of a Bidentetea vegetation. A similar pollen assemblage, at that time not recognized, can be traced in the Hillegersberg diagram of Voorrips (1964). Bidentetea vegetation frequently occurs on clayey wet plains with little organic material (Westhoff & Den Held 1975) and may include Chenopodium glaucum, C. rubrum, C. ficifolium, C. album, C. murale, C. hybridum and C. polyspermum (M. Horsthuis personal communication). P. persicaria-group pollen producing taxa in north-western Europe only include the possible Bidentetea species P. lapathifolium, P. mite, P. minus, P. hydropiper and P. persicaria (Punt et al. 1988). Caryophyllaceae undiff.type pollen in this zone belongs to the Cerastium fontanum- and Moehringia trinervia-group (Punt et al. 1995). The Cerastium fontanum-group contains most north-west European Cerastium and Stellaria species including species present in the Bidentetea (S. media, C. fontanum and C. glomeratum). The Moehringia trinervia-group contains most north-west European Minuartia species, Cucubalus, Honkenya and the possible Bidentetea species Gypsophila muralis (Heukels & Van der Meyden 1983; CBS 1992).

At the beginning of peat accumulation in the residual channel, Bidentetea vegetation will have been present on the clayey natural levees, that were not yet covered with organic material. This hypothesis is supported by the presence of a vegetation horizon (palaeosol) at the top of the clay layer along the margins of the residual channel, extending onto the natural levees (Fig. 2). Also the high (extralocal?) values of *Urtica dioica*-type pollen (including *U. urens* and *U. dioica*) may point to the nearby presence of humid, nutrient-rich conditions.

The vegetation in the residual channel may have witnessed a local increase in Sagittaria sagittifolia and Glyceria fluitans in this zone. This is supported by the much

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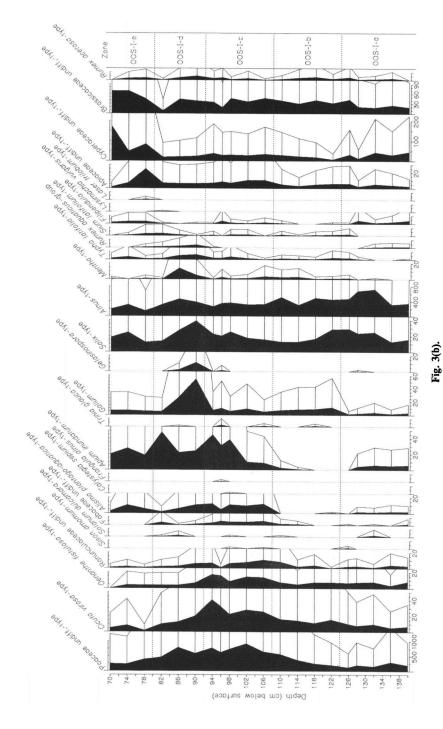


Fig. 3. Wetland pollen percentage diagram of the residual channel section (Oosterwijk I).

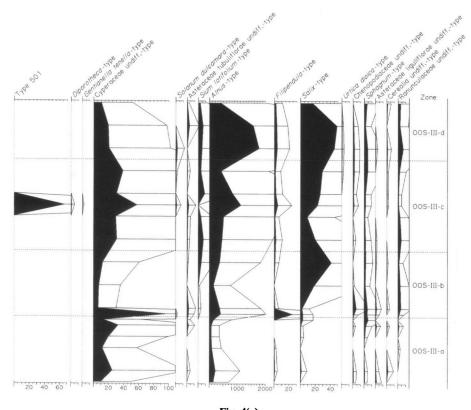


Fig. 4(a).

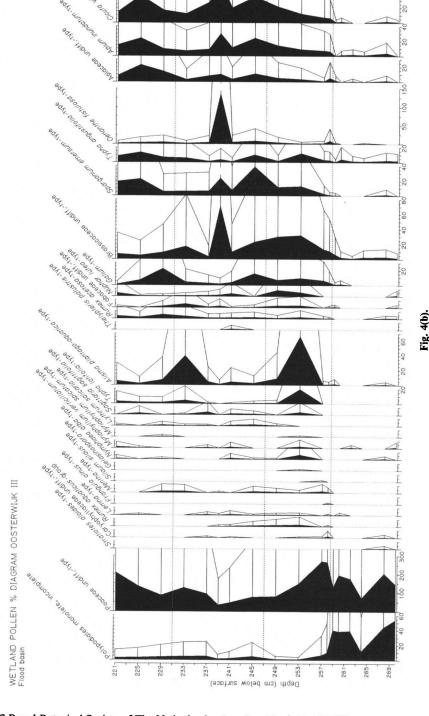
Fig. 4. Wetland pollen percentage diagram of the flood basin section (Oosterwijk III).

lower values of *S. sagittifolia*- and Cerealia undiff.-type pollen (including the wild grass *Glyceria fluitans*, cf. Andersen 1979) in the synchronous OOS-III-d zone.

Zone OOS-I-c (108-92 cm) is characterized by relatively high values of T. angustifolia-, S. emersum-, S. sagittifolia-, Poaceae undiff.-, Cicuta virosa-, Oenanthe fistulosa- (including all north-west European Oenanthe species), Ranunculaceae undiff.-, Fabaceae undiff.-, Alisma plantago-aquatica- (including A. gramineum, A. lanceolatum and A. plantago-aquatica), Calystegia sepium-, Apium inundatum- (including A. graveolens, A. inundatum and A. nodiflorum), Filipendula- and Cyperaceae undiff.-type pollen. This pollen assemblage indicates the presence of a wet phase of terrestrialization dominated by helophytes and other tall macroforbs, possibly forming flotants or floating fringes (Van Donselaar 1961; Westhoff et al. 1971; Den Held et al. 1992).

Zone OOS-I-d (92-80 cm) is characterized by relatively high values of Poaceae undiff.-, Mentha- (including a.o. Mentha and Lycopus), T. latifolia-type and R. aquaticus-group (including R. aquaticus and R. hydrolapathum) and lower values of C. virosa-, O. fistulosa-, A. plantago-aquatica- and Cyperaceae undiff.-type pollen. Very prominent are the synchronous peaks of Gelasinospora-type spores and pollen of Salix-and Galium-type (including all Rubiaceae) at the beginning of the zone, simultaneously with a dip in the curve of Poaceae undiff.-type and Apium inundatum-type. Gelasinospora is an ascomycete indicative for fire (Van Geel 1978), while Salix is considered to be an

40



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element of disturbance in alder carrs (Van der Woude 1983, Wiegers 1992). This may indicate the occurrence of fire in the surroundings of section Oosterwijk I, affecting reed marshes and brushwood along the margins of the residual channel. After this fire a re-establishment of reed marsh vegetation took place, leading to a dominance of Poaceae (probably *Phragmites*), *Galium*, *Mentha* and/or *Lycopus*, *T. latifolia*, *R. aquaticus* and/or *R. hydrolapathum*, *Sium latifolium* and/or *Berula erecta* (both included in the *Sium latifolium*-type) and eventually *Apium*. No clear traces of this fire are visible in the Oosterwijk I upland diagram (De Klerk *et al.* 1997), suggesting that the fire must have swept a limited area.

Zone OOS-I-e (80–70 cm) is characterized by relatively high values of Cyperaceae undiff.- and Brassicaceae undiff.-type pollen. The increase in Cyperaceae undiff.-, together with a decrease of Poaceae undiff.-type pollen values, may suggest somewhat drier conditions in the residual channel as a result of continuing terrestrialization. This is supported by the lithology of the section in which a gradual change from *Phragmites* peat to *Alnus* peat is discernible at this level. The *Alnus*-type pollen curve, however, does not show a synchronous increase. Higher *Alnus*-type values in the peat layers above this zone up to 800%, which are present in a pilot study of the section, indicate that the *Alnus* peat originates from *Alnus* roots penetrating into an older *Phragmites* peat substratum ('Verdrängungstorf', Große-Brauckmann 1979).

Vegetation development in the flood basin

The lithology of section Oosterwijk III (Fig. 2) consists of *Alnus* peat in the upper part (covered by zones b, c and d) indicating either a continuous presence of *Alnus* near the sampling point or the invasion of alder roots from a higher level. The following local wetland zones can be distinguished.

Zone OOS-III-a (270–258·5 cm) is characterized by the absence or relatively low values of most pollen and spore types, except for Polypodiales-type spores, Poaceae undiff.- and Cyperaceae undiff.-type pollen. This zone represents the period of minor river activity in the study area, resulting in the deposition of a clay bed. The pollen assemblage suggests that the flood basin was covered by a marsh vegetation comparable with the subassociation Thelypteridetosum of the Typho-Phragmitetum (Schaminée et al. 1995).

Zone OOS-III-b (258.5–247 cm) is characterized by decreasing values of Poaceae undiff.-type, high values of T. latifolia- and A. plantago-aquatica-, and increasing values of Brassicaceae undiff.-, S. emersum-, O. fistulosa-, A. inundatum-, C. virosa-, and Cyperaceae undiff.-type pollen. This indicates a first phase of terrestrialization as described by Van Donselaar (1961), Westhoff et al. (1971) and Den Held et al. (1992). Also minor peaks of Nymphaea alba-, Myriophyllum verticillatum-, M. spicatum-, S. sagittifolia- and Nuphar lutea-type are perceptible, suggesting a temporal expansion of the open water area. Prominent is the lowermost sample of this zone, containing high values of Poaceae undiff.-, Frangula alnus-, O. fistulosa-, Cyperaceae undiff.-, Solanum dulcamara- and Filipendula-type pollen. This assemblage points to the presence of macrophorb communities growing on the wet and nutrient rich clay deposits in the pioneer phase of peat accumulation (Westhoff & Den Held 1975).

Zone OOS-III-c (247-231 cm) is characterized by relatively high values of Cyperaceae undiff.-type pollen. Values of Poaceae undiff.- and Salix-type pollen show a decrease, followed by an increase. Prominent are the high values of Galium-, S. emersum-, T. angustifolia-, A. inundatum- and C. virosa-type pollen in the lowermost sample of this

zone, indicating a drier phase of terrestrialization (Van Donselaar 1961; Westhoff et al. 1971, Den Held et al. 1992). The increase of Salix-type pollen may point to the expansion of alder/willow carrs, which mainly start with the light-demanding willow species (Wiegers 1992). Sample 239 is characterized by conspicuous peaks of Mentha-, Fabaceae undiff.-, Brassicaceae undiff.-, S. emersum-, T. angustifolia-, O. fistulosa-, A. inundatum-, C. virosa-, Cyperaceae undiff.-, S. dulcamara-, Asteraceae tubuliflorae undiff.-, Alnus- and Filipendula-type pollen and Diporotheca-type fungal spores. Also prominent is the high value of the fungal spore Type 501, of which the ecological significance is unknown (Van Geel et al. 1986). This typical sample probably represents an excrement of an animal, containing pollen of fodder plants and pollen deposited on these plants (cf. Joosten & Van den Brink 1992). This hypothesis seems to be supported by the presence of a large amount of Cercophora-spores in the sample at 239 cm depth, which is indicative for dung (Van Geel 1978; Van Geel et al. 1981; Witte & Van Geel 1985). The excrement hypothesis might be contradicted by the high values of C. virosa-type pollen, a pollen type that in north-western Europe is only produced by the very poisonous species C. virosa (Heukels & Van der Meyden 1983). Cicuta, however, is eagerly eaten by cattle despite its poisonousness, lethal doses for cattle being only 200 g (P. Oosterveld & P.A. Slim, personal communication).

Zone OOS-III-d (231–221 cm) is characterized by high values of Poaceae undiff.-, Alnus- and Salix-type pollen. The high values of S. emersum-, Apiaceae undiff.-, A. inundatum- and C. virosa-type pollen at level 225 are striking, followed by a decrease in values of Alnus-, Salix- and Cyperaceae undiff.-type. An incidental high value of Galium-type pollen is present at level 229. The high percentages of Alnus- and Salix-type pollen point to the late (drier) stage in the vegetation succession.

The subsequent decrease of the values of *Alnus*- and *Salix*-type pollen and the increase in the values of pollen types of plants ascribed to wetter environments at the top of the diagram may point to a regression of the vegetation as a result of more rapidly rising water levels. This latter zone is synchronous with the beginning of peat accumulation in the residual channel, approximately 2700 cal year BP (De Klerk *et al.* 1997).

Although the floodbasin diagram shows a succession similar to present-day terrestrialization, the time period studied (over 1000 years) suggests continuously rising water levels.

CONCLUSIONS

During river activity prior to 3500 cal year BP the flood basin contained reed marshes similar to the present-day subassociation Thypho-Phragmitetum thelypteridetosum, in which clay was deposited. After river activity ceased, the flood basin changed into an extensive eutrophic mire with a vegetation development largely resembling the pattern of present-day terrestrialization with, after an initial macrophorb vegetation, a succession of reed and sedge swamps and eventually an alder/willow carr (c.f. the fluvio-lacustrine environment described by Van der Woude 1983, 1984). Areas of open water inhabited by water plants have also been present. The duration of these terrestrialization phases (encompassing 1000 year), point to a continuous rise of absolute water levels. Grazing of large mammals in these areas is suggested by the presence of a possible excrement found in the core.

The residual channel experienced a phase of minor river activity prior to 2700 cal year BP, during which clay was deposited. At that time the channel contained a vegetation of © 1997 Royal Botanical Society of The Netherlands, Acta Bot. Neerl. 46, 147-159

T. angustifolia and occasionally Sparganium in the deeper water, and reed marshes closer to the upland. After river activity ceased, a pioneer Bidentetea vegetation with Chenopodiaceae, Caryophyllaceae and Polygonaceae invaded the clayey substrate of the lower natural levee margins. This pioneer vegetation was replaced by reed and later sedge marshes and eventually alder forest. During the former phase, a local fire probably swept the area.

Natural levees contained an alluvial hardwood forest, described by De Klerk et al. (1997).

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