

# DIFFERENCES BETWEEN VALLEY AND UPLAND VEGETATION DEVELOPMENT IN EASTERN NOORD-BRABANT, THE NETHERLANDS, DURING THE LATE GLACIAL AND EARLY HOLOCENE

W. VAN LEEUWAARDEN and C.R. JANSSEN

Laboratory of Palaeobotany and Palynology, University of Utrecht, Heidelberglaan 2, 3584 CS Utrecht (The Netherlands)

(Received June 17, 1986; revised and accepted August 28, 1986)

## Abstract

Van Leeuwaarden, W. and Janssen, C.R., 1987. Differences between valley and upland vegetation development in eastern Noord-Brabant, The Netherlands, during the Late Glacial and early Holocene. *Rev. Palaeobot. Palynol.*, 52: 179–204.

Analysis of pollen, including the determination of pollen concentrations and of relative pollen values, macrofossil analysis of peat cores from oxbows in river valleys and of pingo melt holes on the upland, and the application of recent surface samples from northern Finland have enabled the establishment of two different lines of vegetational succession, one for the valley and another for the upland. In the valley, the succession is from *Betula*-, *Betula* + *Populus*-, *Betula* + *Pinus*-, *Pinus* + *Betula* + *Corylus*-, *Pinus* + *Corylus* to *Alnus* + *Tilia*. On the upland, the succession is from *Betula*-, *Betula* + *Corylus*-, *Corylus* + *Quercus* to *Corylus* + *Quercus* + *Ulmus*.

The order of appearance of pollen of the main forest trees is similar in all the pollen diagrams, but they differ in time of appearance. Radiocarbon dates indicate that *Pinus*, *Corylus*, *Quercus*, *Ulmus*, *Tilia* and *Alnus* appear in the valley 300–700 years earlier than on the upland. *Juniperus* occurred mainly on the upland. Taxa that were restricted to the upland include *Empetrum*, *Erica tetralix* and *Arctostaphylos uva-ursi*. *Populus* occurred only on the valleys.

## Introduction

Both in the past and today plant species are not regularly distributed, but are associated with definite vegetation types, depending on local parameters. The primary task of the palaeoecologist is to reconstruct these former vegetation patterns.

Surface-sample studies on the relationship pollen/vegetation (e.g., Aario, 1943; Lichti-Federovich and Ritchie, 1968; Webb and McAndrews, 1976) have shown that pollen assemblages from large-sized bogs and lakes reflect the vegetation on the level of the plant

formation. However, vegetation types of small areal extent can be reconstructed by the study of contrasting sites of various sizes and in different locations (Janssen, 1960, 1967, 1973, 1981, 1984; Jacobson, 1979; De Valk, 1981).

The vegetation surrounding the basin of deposition is better reflected in soils and small-sized basins than in larger peatbogs, which show a regional pollen deposition characteristic for the entire region, regardless of local conditions. The local swamp vegetation is reflected in the local pollen deposition, superimposed on the regional pollen deposition.

Eastern Noord-Brabant is a cover-sand area

dissected by a number of small rivers. In such a landscape, vegetation successions along three separate lines can be distinguished (c.f. also Tüxen, 1931):

(1) A vegetation succession in former beds of streams, generally connected with the process of lake filling: the local succession.

(2) A vegetation succession on azonal soils in the valley, where the groundwater level is high: the lowland succession.

(3) A vegetation succession of the "dry" upland: the upland succession.

The difference in altitude between the valley floor and the upland is small, usually a few meters. The sites that were selected for study are all of small areal extent, viz., oxbows in which the local and lowland successions prevail, and pingo melt holes, small, almost circular lakes, located in the cover-sand area in which, besides a different type of local succession, the upland succession is reflected. Cores from five lowland and two upland sites were analyzed. Only three (Olland and Keldonk, both lowland sites, and Klein Hassels Ven, an upland site) are represented in the abbreviated account in this paper<sup>1</sup>, only the upland diagrams are shown. The combined pollen assemblages of these sites will give insight into the pattern of vegetation in the past.

A number of approaches are useful to enable this palynological contrast to give the desired information.

### (1) Radiocarbon dates

Pollen assemblages with a significant local component are difficult to correlate in time. Similar pollen assemblages may be of different ages, while different pollen assemblages may have the same age. Dating on the basis of similar pollen features is thus unreliable and radiocarbon dating of the various assemblages must be the basis of the establishment of a spatial pattern of vegetation.

<sup>1</sup>This paper is a condensed version of Van Leeuwen (1982).

### (2) Determination of pollen concentration

The time span studied includes the important transition from the open unforested landscape of the Late Glacial to the generally forested aspect of the landscape in the early Post Glacial. During this time, several tree species migrated into the area and important changes took place in the number of pollen grains deposited per unit time and per unit surface. Therefore, pollen-concentration diagrams were constructed in order to determine to what extent the relative decrease of the NAP percentages is due to an increase in the input of arboreal pollen in the basin and to what extent there is a real decrease in non-arboreal pollen. Determination of the pollen deposition per unit time thus enhances the insight into the competition between the immigrating plant species and species already present in the landscape.

### (3) Surface-sample studies

Studies of surface samples from an area that, to some extent, can be considered as a modern analogue of Noord-Brabant during the Late Glacial and early post Glacial were carried out with the aim of aiding the interpretation, in terms of vegetation, of the proportion of *Pinus* and *Betula* pollen in the deposition in small basins. Northern Finland was selected as a suitable area, because here *Pinus* and *Betula* are the dominant tree species and thermophilous trees are absent. Although the vegetation of northern Finland should not be considered as an exact modern analogue of the vegetation of the Late Glacial and early Holocene in Noord-Brabant, this area is the closest extant analogue and, moreover, conclusions from the surface-sample studies can be drawn when only *Pinus* and *Betula* are considered. Although regional surface-sample studies in northern Finland have already been carried out by Aario (1943) and Prentice (1978), studies on the local and extra-local pollen deposition (in the sense of Janssen, 1973) are needed in order to render comparison possible with the pollen

values from the small-sized basins in Noord-Brabant.

#### (4) *Macrofossil analysis*

Pollen can be transported over long distances by the wind, especially when the vegetation is open. It is therefore not always easy to determine whether the presence of high pollen values in a sample is an indication of local presence, or whether the pollen was transported to the coring site from elsewhere. In contrast, most macrofossils are not easily transported by wind. Surface-sample studies by Birks (1973) indicate that only seeds of *Betula* and, to a lesser extent, seeds and needles of *Pinus*, can be dispersed by the wind and that in limnic sediments most of the macrofossils are transported by water currents. From this it follows that macrofossils in peats are least likely to have been transported by water and that the source is very local, probably the mire itself.

This study deals with the Late Glacial and early Holocene and can be considered as a complement to studies in the late post Glacial of the same area of Noord-Brabant (Janssen, 1972).

In this paper, the *Alnus* expansion is considered to indicate the establishment of the edaphic climax and the final phase of the hydrosere, more or less coinciding with the establishment of the "climax" deciduous forest on the upland. The increase of *Alnus* pollen and the decrease of *Pinus* pollen in the diagrams is therefore an obvious point in time at which to place the upper limit of the investigations. Only the succession on the upland and valley floor will be discussed here. The hydroseres will be accounted for in a later paper. The pollen diagrams presented include, therefore, only the pollen types from plant species in upland and flood-plain habitats.

#### Sites

The location of the coring sites is shown in Fig.1. Five cores from small-sized mires come

from the valley floor: Olland, Keldonk, Everse Moerkuilen A en B and Gemonde, all between 15 and 40 m from the upland. Two cores are from small pingo melt holes; Klein Hassels Ven and Strabrechts Rond Veen, 35 and 10 m from the upland, respectively. Only the upland pollen diagrams of Olland, Keldonk and Klein Hassels Ven are fully reproduced here.

#### Material and methods

The cores were collected with a gauge of 7 cm diameter for the upper 2 m and with a Dachnovsky sampler with a diameter of 6 cm for the deposits below 2 m.

The cores were longitudinally divided into two equal parts in the laboratory; one for the pollen analysis and the second for the analysis of macrofossils and for radiocarbon dating.

#### *Pollen analysis*

Pollen analysis included boiling with 10% KOH, sieving through a fine screen (250  $\mu$ m mesh) and acetolysis at 98°C for 6 min. Sand was removed with hydrofluoric acid. The material was mounted in silicone oil 2000 CS, without stain.

Whole slides were counted to avoid the effect of unequal distribution of pollen and spores under the cover glass (Brooks and Thomas, 1967).

#### *Macrofossil analysis*

The part of the core used for macrofossil analysis was cut into slices of 5 cm length, placed in 10% KOH for several days at room temperature and differentially sieved (meshes successively 2–0.5 mm); meshes smaller than 0.5 mm could not be used because of plugging.

#### *Relative pollen diagrams (Figs.2–7)*

The percentages of the taxa were calculated on the basis of a pollen sum which includes all types of upland plant taxa; these include taxa which are unlikely to have been present in the

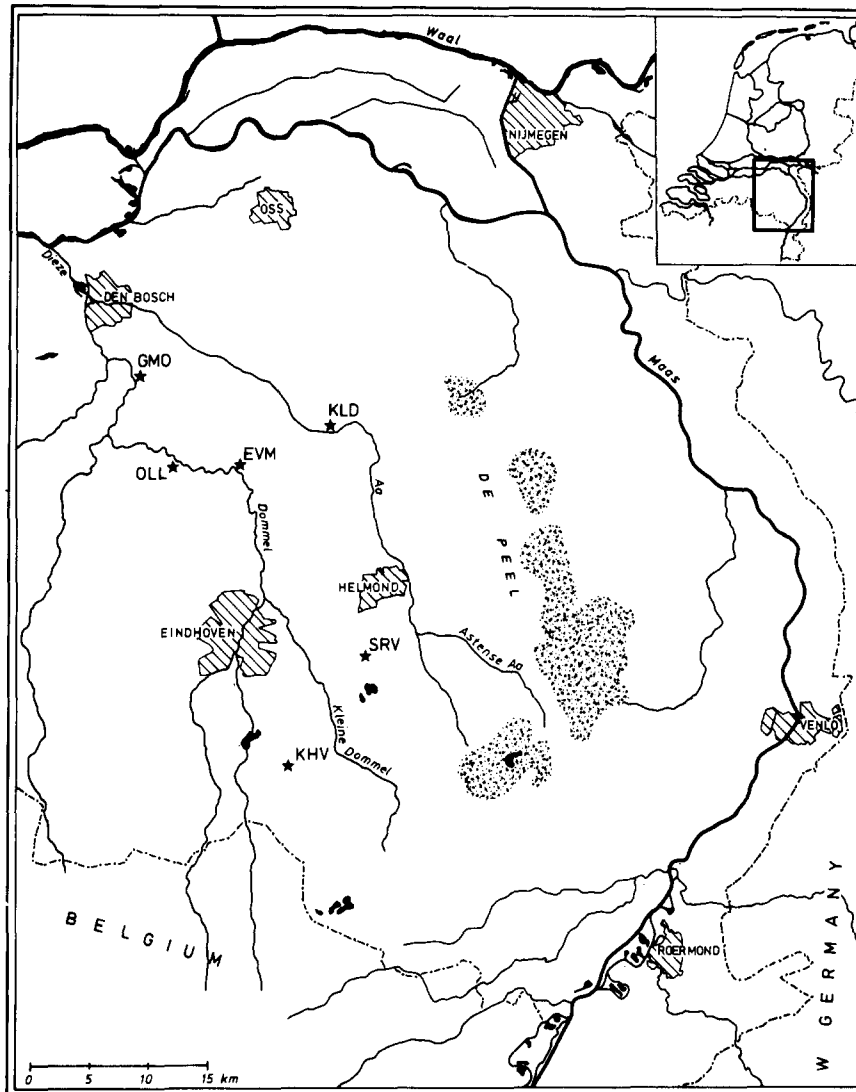


Fig.1. Location of the coring sites in Noord-Brabant. *EVM* = Everse Moerkuilen; *KHV* = Klein Hassels Ven; *KLD* = Keldonk; *GMO* = Gemonde; *OLL* = Olland; *SRV* = Strabrechts Rond Veen.

mire itself. Pollen of *Poaceae* and *Cyperaceae* may very well have come from the mire vegetation and these types were therefore excluded from the pollen sum. All curves are drawn to a standard scale for each pollen diagram, shown at the bottom of the diagram. The unshaded curves are the actual values; the grey shaded curves, the black shaded curves and the broadly striped shaded curves show exaggerations of 5, 25 and 125 times, respectively.

The pollen types have been arranged into three groups: (1) trees and shrubs; (2) forest herbs and (3) herbs from open, non-forested vegetation.

#### *Pollen concentration diagrams (Figs.8–11)*

For the determination of pollen concentration, the material was weighed prior to the addition of known amounts of pollen of taxa

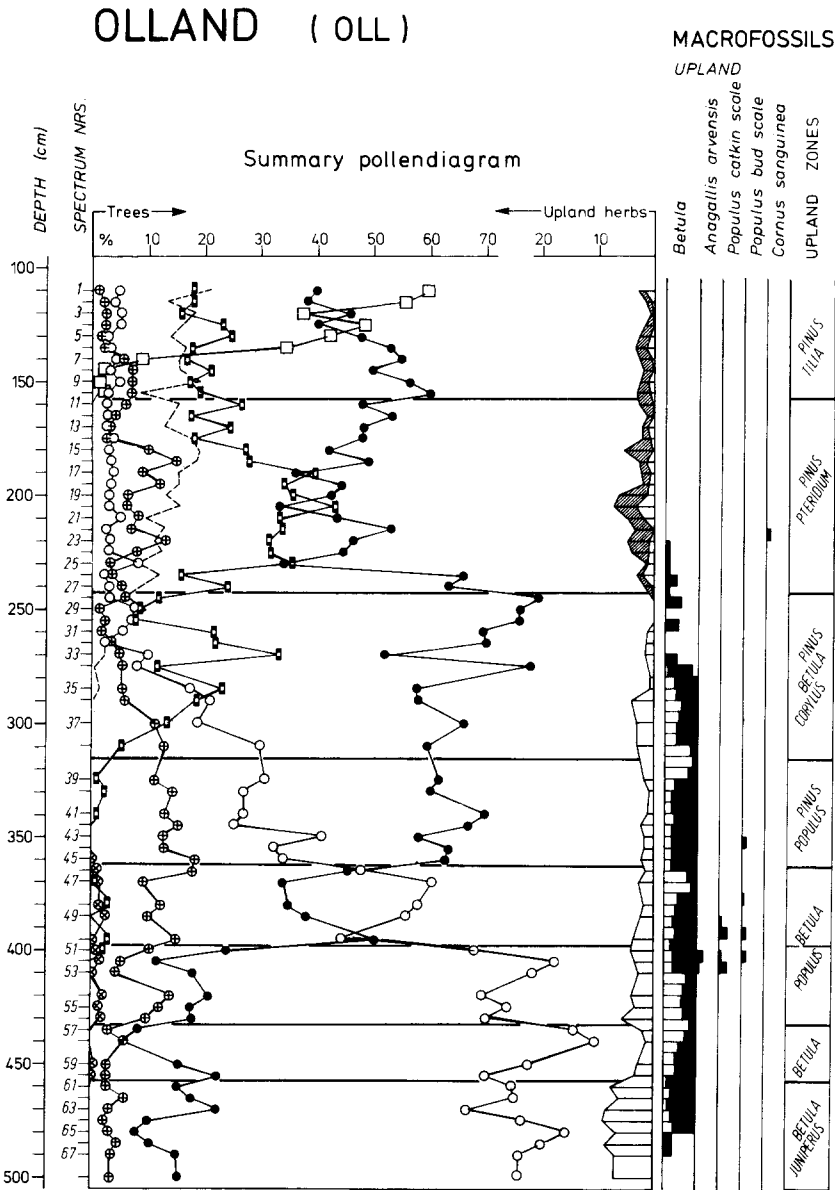


Fig.2. Summary pollen diagram, macrofossil diagram of upland types and regional pollen zones of Olland.

that are unlikely to have been present in the area (exotics). Two types were used: pollen of *Eucalyptus* (Benninghoff, 1962; Matthew, 1969) or spores of *Lycopodium* (Stockmarr, 1971), which can be distinguished from fossil *Lycopodium* spores because the added spores were acetolyzed twice and had become extremely dark in color. The pollen concentration stan-

dardized per gram wet material equals:

$$P_{\text{conc}} = \frac{E_a}{E_b} P_s$$

in which:  $P_{\text{conc}}$  = the unknown concentration of fossil pollen;  $E_a$  = the number of exotics added to the sample;  $E_b$  = the number of exotics counted in the sample;  $P_s$  = the number of



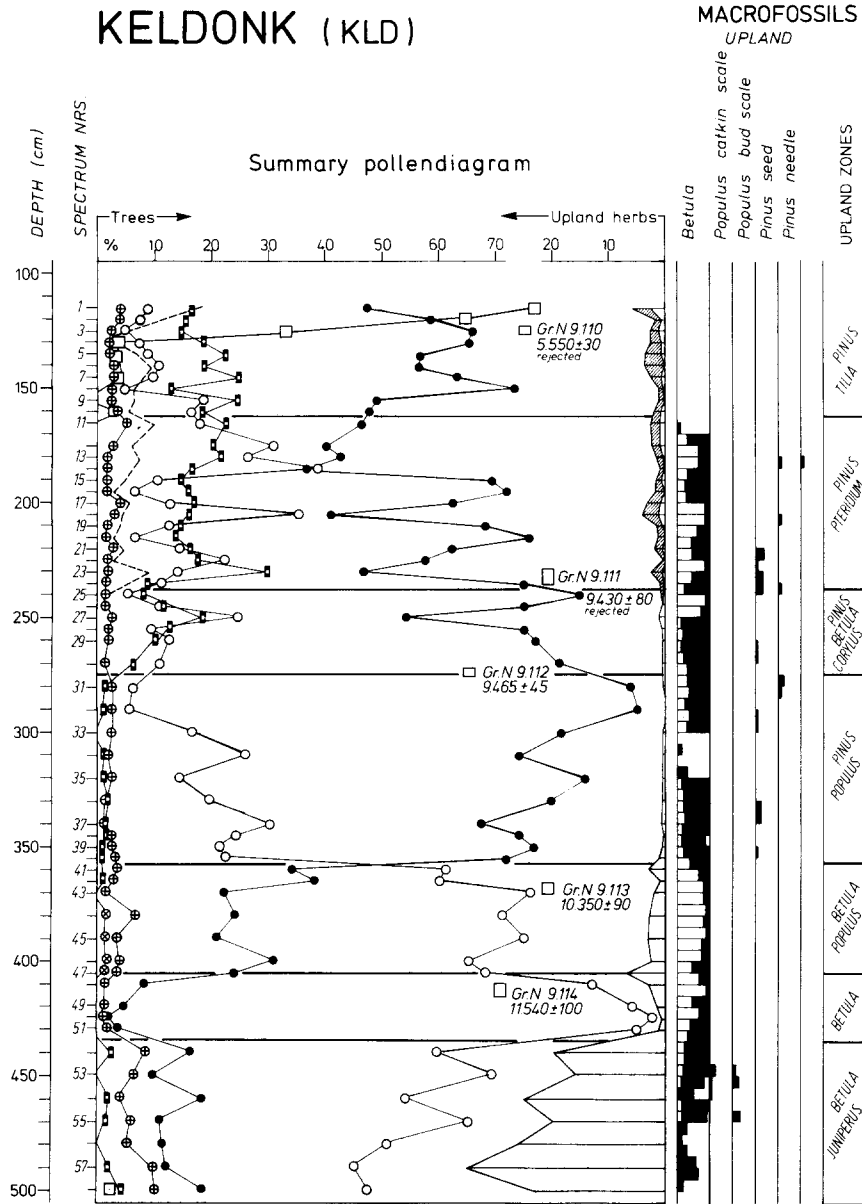


Fig.4. Summary pollen diagram, macrofossil diagram of upland types and regional pollen zones of Keldonk.

fossil pollen counted in the sample. The number of pollen grains per unit volume or weight is the net result of differences in the accumulation rates of the sediment and differences in pollen deposition. In order to determine the deposition of pollen independently of this accumulation rate, the number of pollen

deposited per unit time must be established. Time control is thus essential in this procedure.

However, the number of radiocarbon dates is considered to be too low to allow construction of reliable pollen deposition diagrams. In the peat samples studied here, the concentration

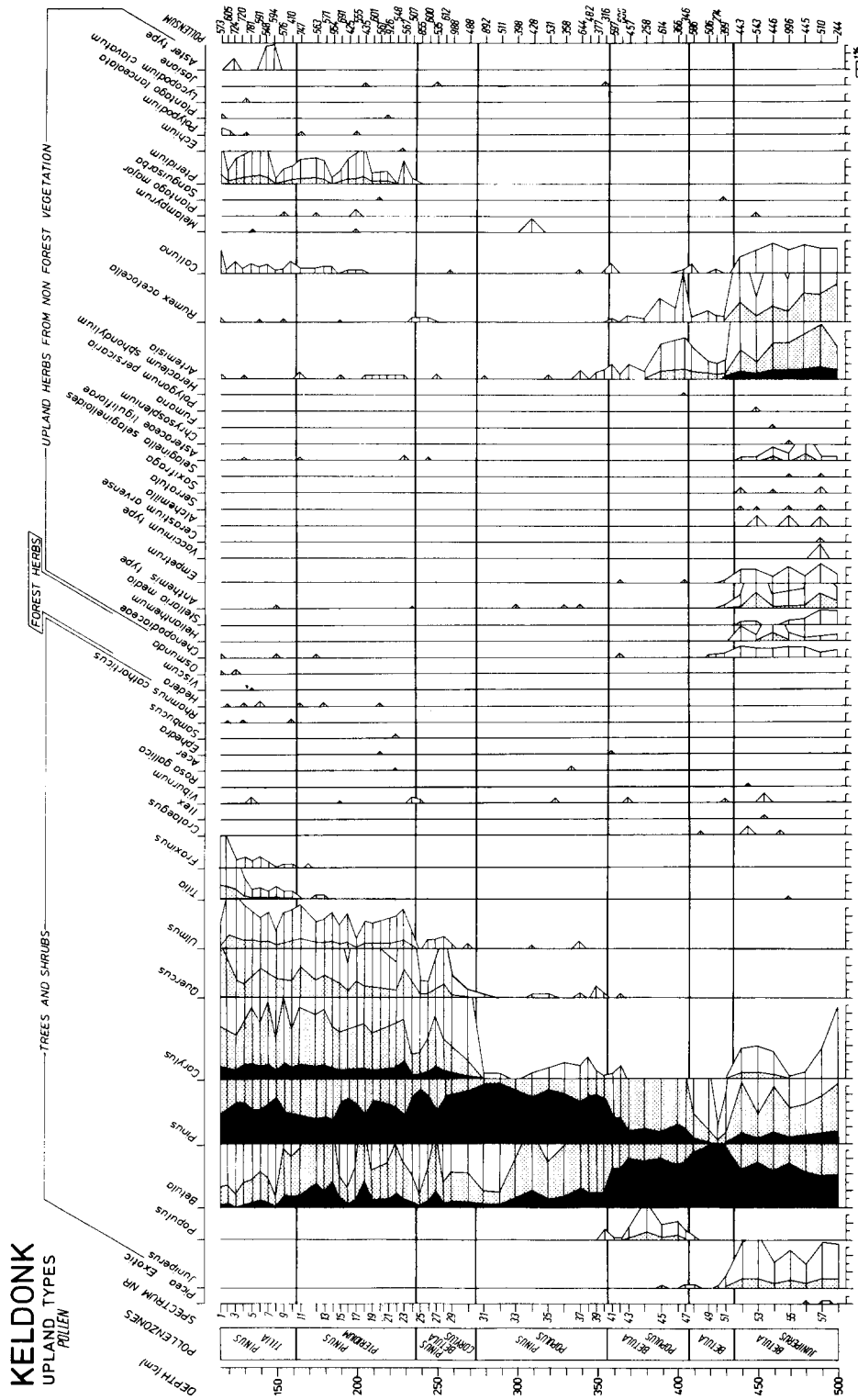


Fig.5. Pollen diagram of upland pollen types of Keldonk.



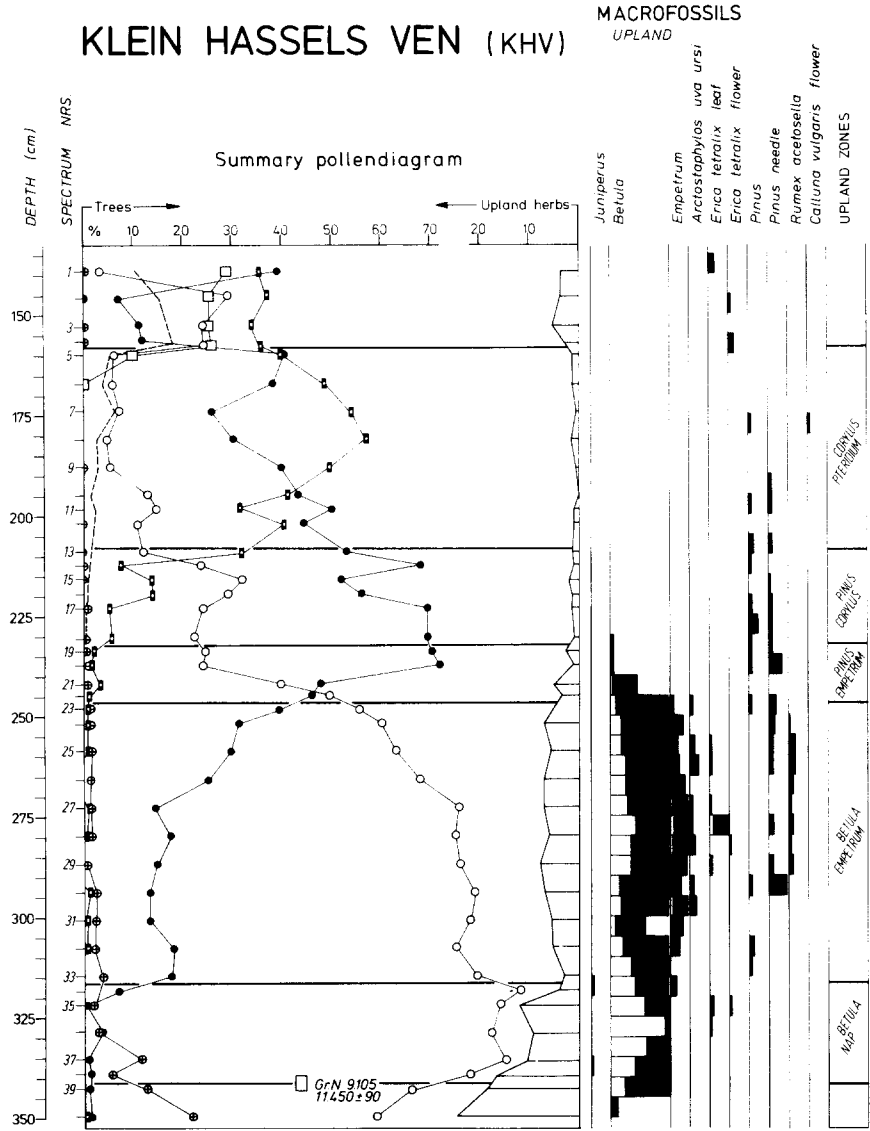


Fig.6. Summary pollen diagram, macrofossil diagram of upland types and regional pollen zones of Klein Hassels Ven.

values often differ strongly, sometimes by more than a factor of 10. Apparently, the sedimentation rate of these lowland peats can change over very short distances in the core. Under these conditions, the determination of pollen deposition per unit time is not reliable.

In contrast, in lake sediments the concentration values do not show these large differences. However, for the part of the core where lake sediments prevail, only one or two radiocar-

bon dates were available; a number too low to determine changes in the sedimentation rate. For these reasons, influx diagrams were not prepared and only concentration diagrams are presented. Despite the lack of sufficient time control to establish deposition values, it is assumed that concentration values mostly reflect changes in the pollen deposition, not changes in the accumulation rate of the sediment.

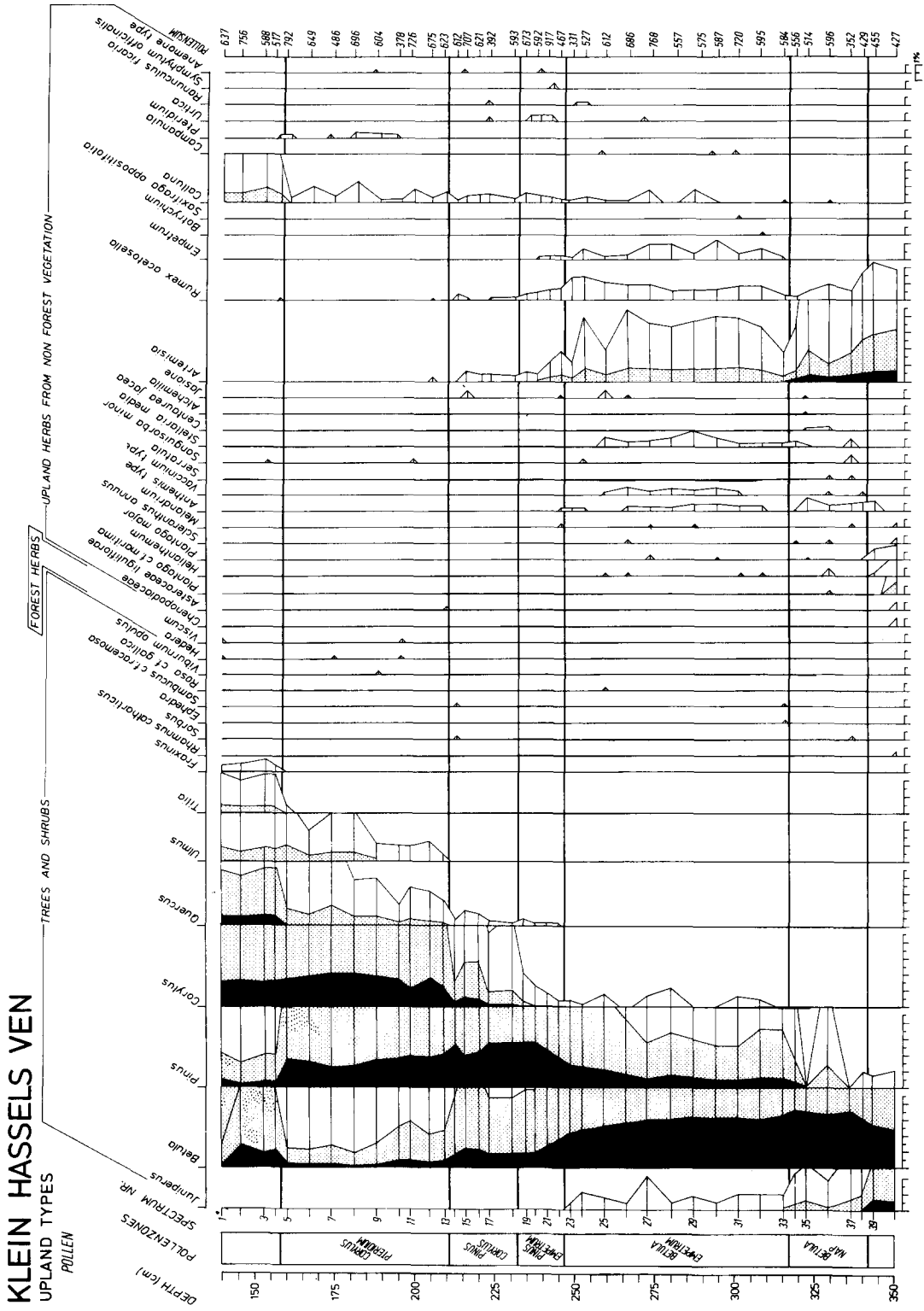


Fig. 7. Pollen diagram of upland pollen types of Klein Hassels Ven.

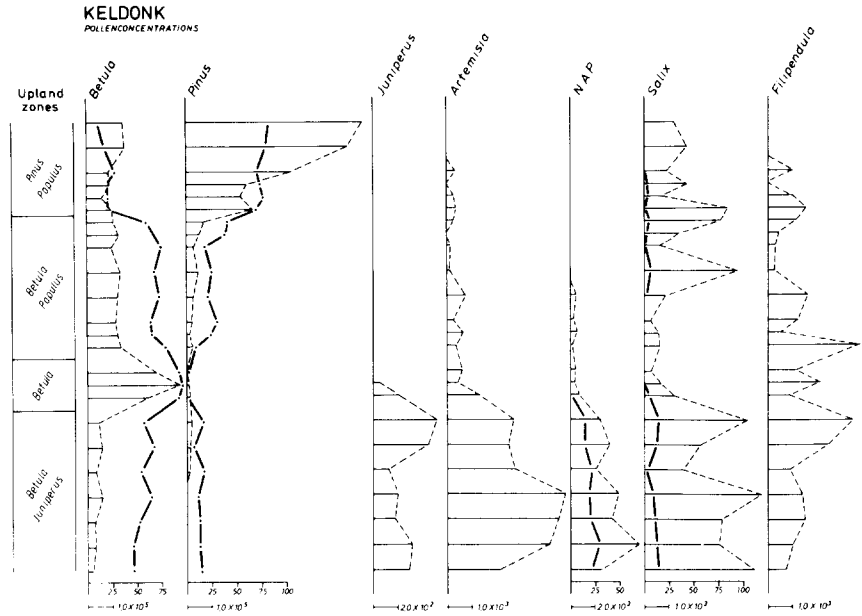


Fig.8. Concentration (---) and relative (—) pollen values of Keldonk.

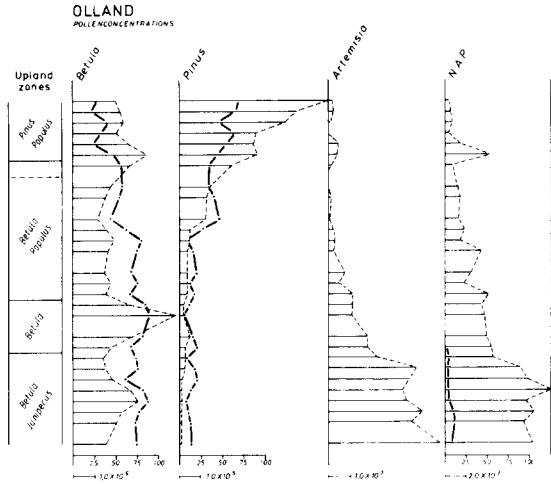


Fig.9. Concentration (---) and relative (—) pollen values of Olland.

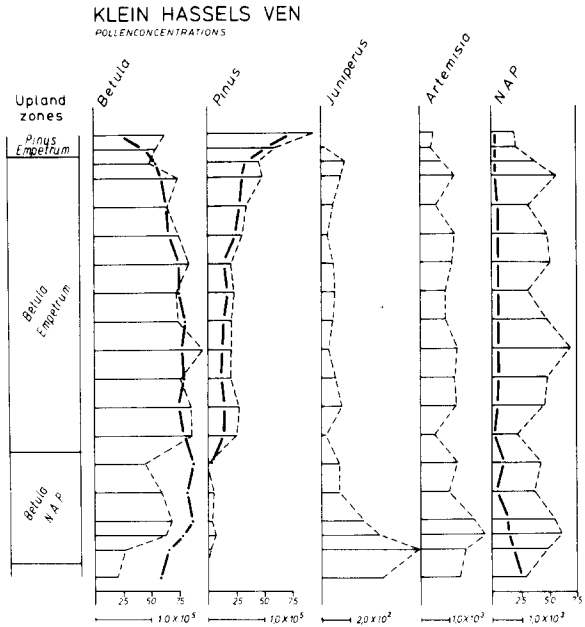


Fig.10. Concentration (---) and relative (—) pollen values of Klein Hassels Ven.

The rationale for this assumption lies in the fact that sudden changes in the concentration values related to sediment types were not observed. The concentration values are shown for a limited number of pollen types (*Betula*, *Pinus*, *Artemisia*, *Corylus* and NAP) together with the relative values in Figs.8–11, and only

the pollen concentrations of Olland, Keldonk, Klein Hassels Ven and Strabrechts Rond Veen have been reproduced.

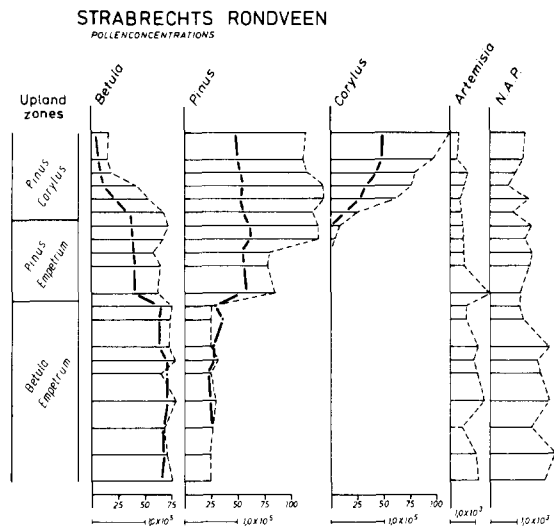


Fig.11. Concentration (---) and relative (....) pollen values of Strabrechts Rond Ven.

### Macrofossil diagrams

The new macrofossils of upland and flood-plain origin are shown next to summary diagrams, enabling a ready comparison of the values of upland macro- and micro-fossils. Since the number of macrofossils found in a sample, compared with the number of pollen grains, is very small, no "seed sum" was established. Instead, the observed number of macrofossils was recorded and standardized per 100 cm<sup>3</sup> material. Wood fragments were often larger than 5 cm and thus filled a large part of the core column. These remains are, therefore, the least likely type of macrofossil to represent a predetermined number of plants. For this reason, wood fragments are not listed in the macrofossil diagram.

### Zonation of the diagrams

Pollen diagrams were zoned to facilitate comparison and discussion. Following Cushing (1967), the upland regional pollen assemblages are named, defined and described in accordance with the International Stratigraphic Guide (Hedberg, 1975). The concentration and macrofossil diagrams are not zoned separately,

but the zones of the relative upland diagrams have been used. Zones are informally established on the assumption that they reflect definable vegetation types or a definable constellation of vegetation types in the landscape. (pollen and macrocoeno-assemblages, Janssen, 1981.)

### Pollen analysis of surface samples in northern Finland

Surface samples from moss polsters were collected at different locations along short transects in the various broad vegetation zones in northern Finland (Fig.12). The transects can be separated in the following groups:

- I. Transects in the *Pinus* forest belt (Wood Lapland) from *Betula* out into the *Pinus* forest.
  - Ia. Transects from a solitary *Betula* tree.
  - Ib. Transects from small *Betula* stands (3–5 trees).



Fig.12. Vegetation formations in northern Finland (after Kalela, 1958). Numbers refer to locations of the surface-sample trajectories.

II. Transects in the *Betula* forest belt (Fjell Lapland) from *Pinus* out into the *Betula* forest.

IIa. Transects from a solitary *Pinus* tree (usually on the upland).

IIb. Transects from small stands of *Pinus* trees (3–5 trees).

IIc. Transects from larger stands of *Pinus* trees (10–20 trees) usually in the valleys.

III. Transects in the tundra vegetation near the river Tena (Tana) at the border between Norway and Finland. In this region, much of the *Betula pubescens* ssp. *tortuosa* vegetation is damaged by caterpillars (*Operinia autumnale*) resulting in a tundra-like vegetation at relatively low altitudes.

IIIa. Transects from a solitary *Pinus* tree.

IIIb. Transects from a small *Betula* stand.

The regional, local and extra-local pollen percentages are shown in Tables I and II. They are based on a pollen sum excluding *Alnus* (not present during the Late Glacial and early Holocene) and *Salix* and *Ericaceae*, often locally over-represented in the surface samples from Finland.

Transect diagrams (not all included in this paper) indicate that regional pollen values are reached in all samples at least 30 m from individual pollen sources (Fig.13). The values in Table I therefore include those from samples beyond this 30 m limit.

### Results

#### Regional values

As may be expected (Aario, 1943), areas with *Pinus* forests and *Betula* forests show large

TABLE I

Recent regional pollen values (%) of *Pinus* and *Betula* in transects under various vegetational conditions in northern Finland

Vegetation belt	Transect group	Transect	Regional pollen values (%)		Mean NAP values
			<i>Pinus</i>	<i>Betula</i>	
<i>Pine forest</i>					
	Ia	1	84	14	8
		2	82	16	6
	Ib	3	80	18	5
		4	80	15	7
		5	82	18	4
<i>Birch forest</i>					
	IIa	6	16	82	8
		7	6	90	3
	IIb	8	18	80	5
		9	16	82	3
		10	13	84	3
		11	18	80	10
	IIc	13	20	78	8
		12	33	60	3
		14	30	66	10
<i>Tundra</i>					
	IIIa	16	28	62	55
		17	30	63	32
	IIIb	15	35	60	29

TABLE II

Recent local and extra-local relative pollen values of *Pinus* and *Betula* in transects under various vegetational conditions in northern Finland

Vegetation belt	Transect group	Transect	Local pollen values (%)					
			<i>Pinus</i>	<i>Betula</i> <sup>a</sup>	<i>Pinus</i>	<i>Betula</i> <sup>b</sup>	<i>Pinus</i>	<i>Betula</i> <sup>c</sup>
<i>Pine forest</i>								
solitary <i>Betula</i>	Ia	1			78	20	81	18
		2			62	32	63	30
small <i>Betula</i> stand	Ib	3	49	49	63	36	62	35
		4	56	42	64	34	76	20
		5			76	24	72	29
<i>Birch forest</i>								
solitary <i>Pinus</i>	IIa	6			65	35	32	68
		7			21	77	19	79
small <i>Pinus</i> stand	IIb	8	62	29	51	49		
		9	70	24	45	53	24	73
		10	77	20	43	47		
		11	76	23			28	70
large <i>Pinus</i> stand	IIc	13	78	20	54	42	44	53
		12	71	27	78	20	43	56
		14	69	30	64	35	46	54
<i>Tundra</i>								
solitary <i>Pinus</i>	IIIa	16	6	92	25	61	29	68
		17			20	80	20	8
small <i>Betula</i> stand	IIIb	15	49	46	43	51	43	54

<sup>a</sup>Inside patch of *Pinus* or *Betula*.

<sup>b</sup>At the margin of patch of *Pinus* or *Betula*.

<sup>c</sup>About 5 m from a patch of *Pinus* or *Betula*.

differences in the regional *Pinus* and *Betula* pollen values. In the *Pinus* forest, *Pinus* shows a regional percentage of about 80%; that of *Betula* is lower than 20%. Almost similar values were observed by Prentice (1978) in this region. Also, the NAP values observed by Prentice are rather similar to our mean NAP values.

Samples from the *Betula* forest belt show regional pollen values of 70–80% *Betula* and 20–30% *Pinus*.

In the samples from the tundra belt, *Betula* pollen is about 60% and *Pinus* about 30%. Similar percentages can be found in the *Betula* vegetation belt in the case of the presence of large *Pinus* stands. The only way to differentiate between the tundra and *Betula* vegetation belts lies in the much higher regional NAP

values in the tundra. These results agree essentially with those of Aario (1943) and Lichti-Federovich and Ritchie (1968).

#### *Local and extra-local values*

Table II shows the local and extra-local values of *Pinus* and *Betula* inside the stand, at the margin of the stand, and at a distance of about 5 m from stand (3). Where only one tree is involved, pollen values from moss polsters underneath the canopy of that tree are listed in category 2.

The following may be concluded from Table II: Transect group I, *Betula* in *Pinus* forest. The local pollen values of *Betula* are equal to those of the regional *Pinus* values inside a small patch of *Betula* trees. Already at the margin of the *Betula* stand and even more

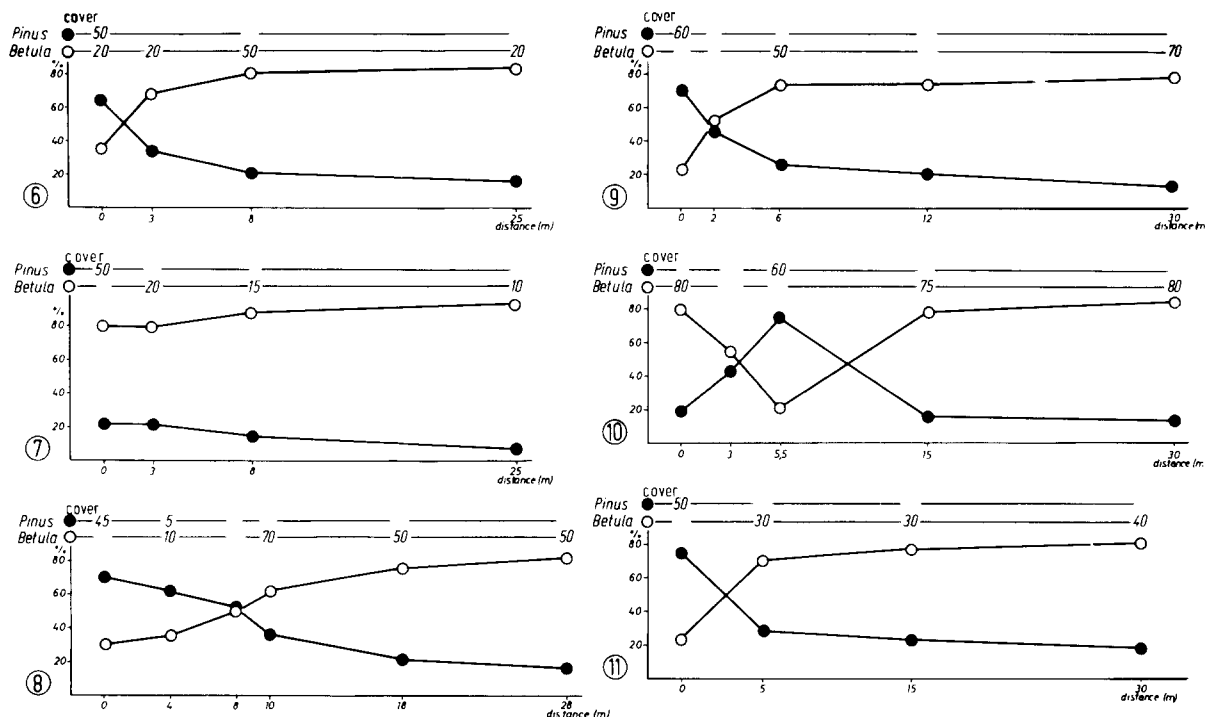


Fig.13. Cover in vegetation and relative pollen values of *Pinus* and *Betula* along surface sample transects nr.6–11 (transect group IIa and IIb).

so away from *Betula*, the strongly decreased *Betula* pollen values indicate that the overall vegetation of the area is dominated by *Pinus*. However, a single *Betula* tree inside a *Pinus* forest does not show such a local effect.

Transect group II, *Pinus* in a *Betula* forest. Fig.13 (transects 6, 7) shows that the extra-local effect of a single *Pinus* tree is weak. However, small stands of *Pinus* show a strong extra-local effect. (Fig.13, transects 8–11).

It is difficult to conclude from the local pollen deposition whether the samples come from a *Betula* forest with some *Pinus* trees, or from a *Pinus* forest with some *Betula* trees. In both cases, the proportions of *Betula* pollen and *Pinus* pollen are almost similar. However, at five meters from a small *Pinus* stand, *Betula* pollen begins to dominate in the pollen assemblage, suggesting the presence of a surrounding *Betula* forest.

Inside and along the margin of large stands of *Pinus* in a *Betula* forest (IIc), *Pinus* pollen is

dominant in the pollen assemblages. At 5 m from the stand, the *Betula* pollen values slightly exceed those of *Pinus*. At this distance from the *Pinus* stand it is difficult to conclude that the samples reflect a *Betula* forest with only some pine stands.

Transect group III, *Pinus* and *Betula* in a tundra vegetation. A *Betula* and a *Pinus* tree in a tundra vegetation show a much stronger local effect than they do inside a forest, preventing the recognition of a tundra vegetation at distances close to these local pollen sources. Here, the high NAP values and the identification of *Betula nana* are necessary to recognize a tundra type of vegetation.

### Pollen analysis of upland and flood-plain cores in Noord-Brabant

#### Correlation of pollen assemblages in time

The basis of correlation is the pollen zone. Twelve pollen assemblage zones were recog-

nized and defined on the basis of the relative pollen values of the pollen types *Juniperus*, *Betula*, *Populus*, *Pinus*, *Empetrum*, *Ulmus*, *Pteridium*, *Tilia* and on NAP total (Table III). The definitions are chosen in such a way that the zone boundaries are parallel to the levels of the empirical limits (limit where expansion begins) of *Pinus*, *Corylus*, *Ulmus* and *Tilia*. In this way, the assemblage zone system can be compared with zones defined by Firbas (1949) for Central Europe.

Fourteen radiocarbon dates of the contacts

of the assemblage zones were obtained; nine for two cores from mires in flood-plain locations and five from two pingo melt holes on the upland. In Fig.14 the zones are plotted against a linear time scale. It appears that the pollen assemblages are diachronous. The figure demonstrates that vegetation changes, as reflected by pollen, occur on the upland a few hundred years later than in the valleys. Apparently, the vegetation dynamics in upland and lowland situations were quite different and the mosaic of vegetation types at any time

TABLE III

Definitions of pollen assemblage zones recognized for valley and upland cores. Ages of the zones in decreasing order from left to right, numbers refer to pollen percentages

	Pollen assemblage zones of valley cores						
	<i>Betula</i> – <i>Juniperus</i>	<i>Betula</i>	<i>Betula</i> – <i>Populus</i>	<i>Pinus</i> – <i>Populus</i>	<i>Pinus</i> – <i>Betula</i> – <i>Corylus</i>	<i>Pinus</i> – <i>Pteridium</i>	<i>Pinus</i> – <i>Tilia</i>
<b>Pollen types</b>							
NAP	8–35	2–3	1–4	2	2	5–7	2–7
<i>Juniperus</i>	1–4		up to 1				
<i>Populus</i>	up to 1		2	0.2			
<i>Betula</i>	45–85	80–98	60–84	60–6	30–4	5	4–17
<i>Pinus</i>	up to 20	2–8	16–25	35–80	50–90	25–75	70–50
<i>Corylus</i>					3–30	15–40	20–12
<i>Quercus</i>					1–10	2–20	5–15
<i>Ulmus</i>						1–3	1–3
<i>Pteridium</i>						5	5
<i>Tilia</i>							0.2–3
<i>Alnus</i>							
	Pollen assemblage zones of upland cores						
	<i>Betula</i> NAP	<i>Betula</i> – <i>Empetrum</i>	<i>Pinus</i> – <i>Empetrum</i>	<i>Pinus</i> – <i>Corylus</i>	<i>Corylus</i> – <i>Pteridium</i>		
<b>Pollen types</b>							
NAP	4–14	4–6	5–3	up to 1			
<i>Juniperus</i>	0.5–5						
<i>Empetrum</i>		0.3–1.5	up to 1				
<i>Betula</i>	75–86	45–76	50–25			5–15	
<i>Pinus</i>		15–45	50–75	45–75		25–50	
<i>Corylus</i>				5–50		40–60	
<i>Quercus</i>						0.5–5	
<i>Ulmus</i>						0.5–5	
<i>Pteridium</i>						up to 2	
<i>Tilia</i>							
<i>Alnus</i>							



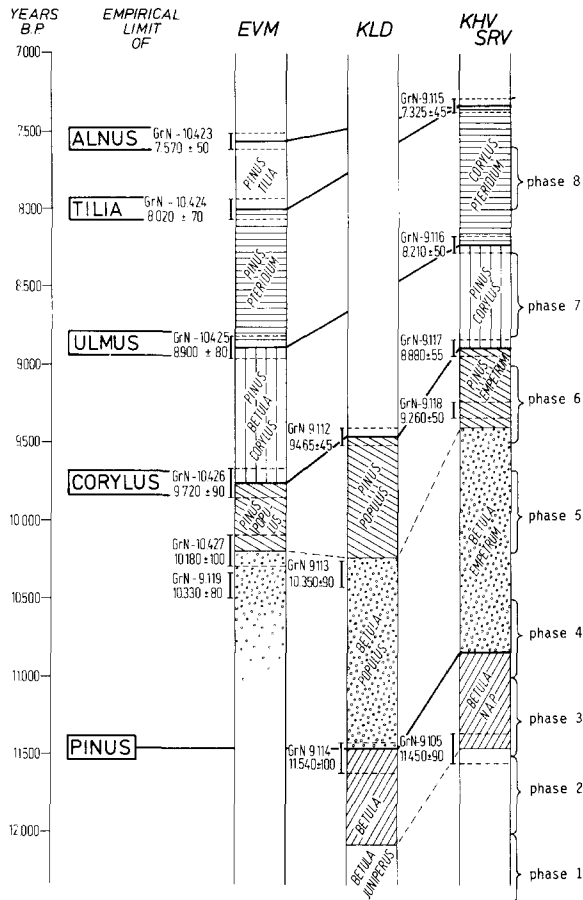


Fig.14. Time correlation of the assemblage zones of the valley cores Everse Moerkuilen (EVM) and Keldonk (KLD) and those of the pingo melt holes Strabrechts Rond Veen and Klein Hassels Ven (SRV/KHV).

was more complex than expected. In fact, much of the complexity in the vegetation development would have gone unnoticed without the availability of radiocarbon dates. Under these conditions, it would be useless to discuss the vegetation development on the basis of the usual zone-scheme. Instead, an attempt to reconstruct the pattern of vegetation will be made on the basis of chronology. The time span covered by the diagrams, roughly 12,000–7300 yr B.P., will be divided into nine phases and the vegetation development will be discussed for each phase with the aid of the relative and concentration diagrams, the macrofossil diagrams and the surface samples from northern Finland. Table IV summarizes phases and assemblage zones for the two types of sites.

#### Discussion of vegetational interpretation of phases

##### Phase 1: Prior to 12,000 yr B.P. (Fig.15.A)

The assemblage zone of the valley cores is the *Betula–Juniperus* assemblage zone, characterized by high pollen values of *Betula* (45–80%) and high values of the NAP (8–35%). *Pinus* pollen values are below 20%. The very low pollen concentration values of *Pinus* indicate that it was absent in the vegetation of that time. *Betula* must have been rather significant in the vegetation, showing high

TABLE IV

Time-phases in the vegetational development and related pollen assemblages in valley and upland cores

Phase	Periods (yr B.P.)	Pollen assemblage zones	
		valley cores	pingo melt hole cores
1	prior to 12,000	<i>Betula–Juniperus</i>	
2	12,000–11,500	<i>Betula</i>	
3	11,500–11,000	<i>Betula–Populus</i>	<i>Betula</i> NAP
4	11,000–10,500	<i>Betula–Populus</i>	<i>Betula–Empetrum</i>
5	10,200–9700	<i>Pinus–Populus</i>	<i>Betula–Empetrum</i>
6	9500–9000	<i>Pinus–Betula–Corylus</i>	<i>Pinus–Empetrum</i>
7	8800–8300	<i>Pinus–Pteridium</i>	<i>Pinus–Corylus</i>
8	8000–7600	<i>Pinus–Tilia</i>	<i>Corylus–Pteridium</i>
9	7600–7300	<i>Pinus–Tilia (+ Alnus)</i>	<i>Corylus–Pteridium</i>

pollen concentration values and the presence of many seeds.

The surface samples from northern Finland (transect group III) indicate that these high

relative pollen values of *Betula* are possible in rather open vegetation types.

Unlike in northern Finland today, there was probably not a tundra matrix. The occurrence

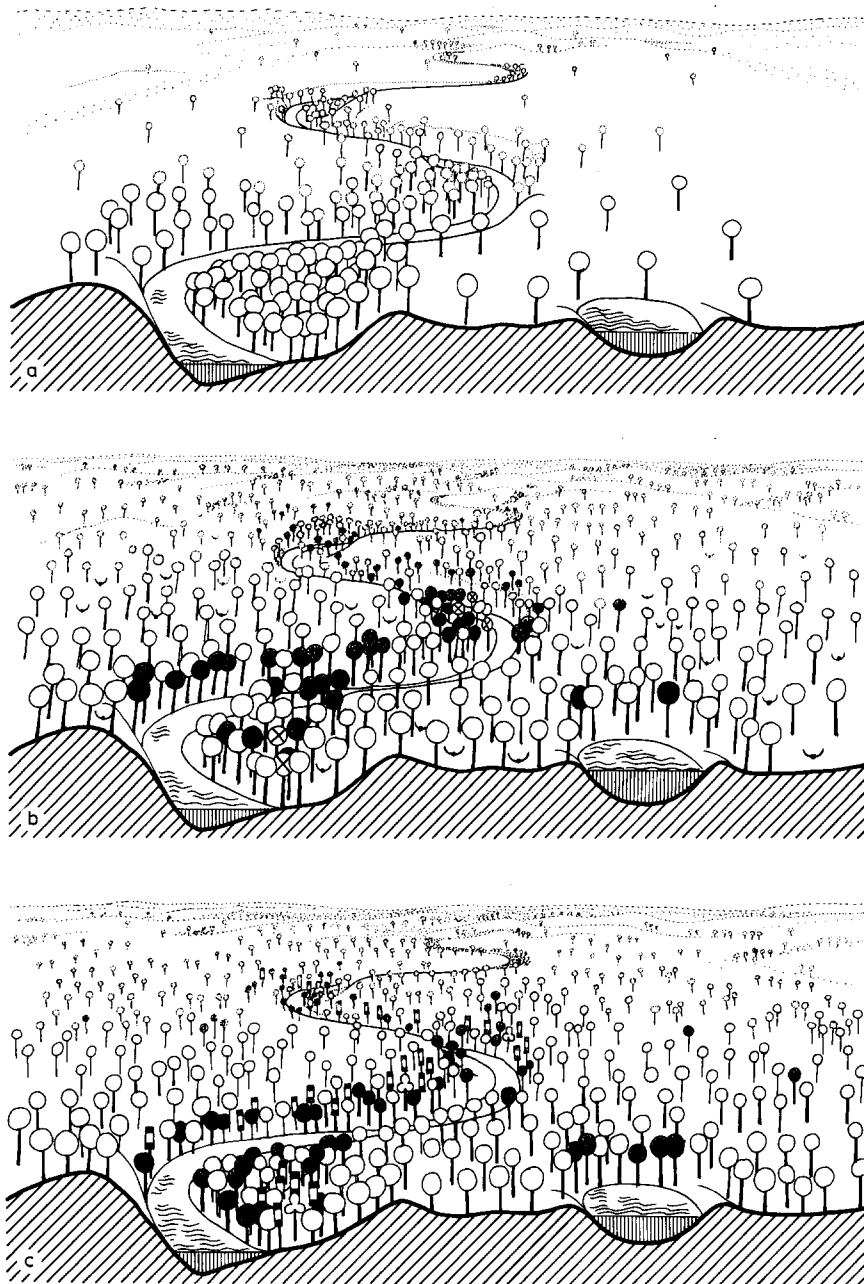


Fig.15. Simplified interrelation between lines of succession in valley and on upland in eastern Noord-Brabant during some fixed time intervals: a. 12,000–11,500 yr B.P.; b. 11,000–10,500 yr B.P.; c. 9600–9000 yr B.P.; d. 8800–8300 yr B.P.; e. 7600–7300 yr B.P.

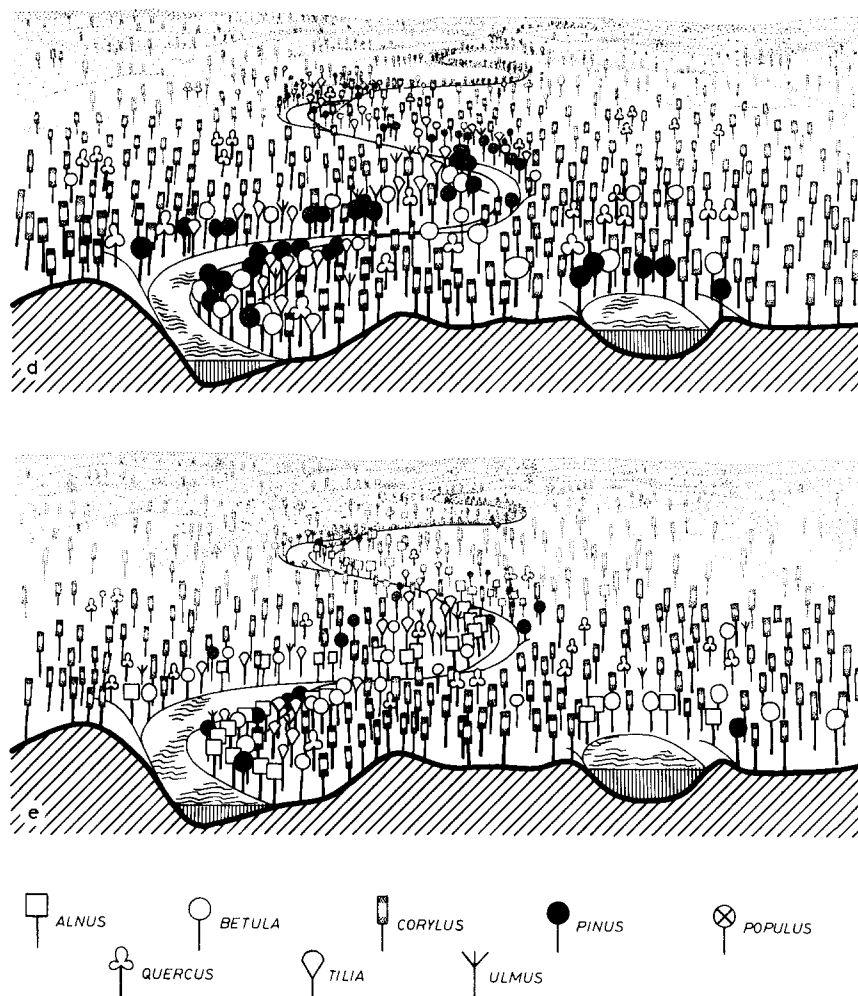


Fig.15. Continued.

of pollen of *Polemonium*, *Helianthemum*, *Artemisia*, Asteraceae liguliflorae and Caryophyllaceae point to a steppe matrix in which scattered *Betula* trees may have been present.

Apart from *Betula*, also *Populus* (macrofossils and pollen) and *Salix* were locally present. These trees are typical for flood-plain situations (e.g., analogous to a *Populus*-rich SALICION today). Although no material of this age was available at the upland sites, it is, analogous to the next phase samples, likely that on the upland a steppe vegetation with *Juniperus* and some scattered *Betula* trees was present.

#### Phase 2: 12,000–11,500 yr B.P.

(a) Valley. This time span is covered by the *Betula* assemblage zone. It is characterized by high pollen values of *Betula* (80–98%) and very low NAP values. Both the concentration pollen diagrams and the macrofossil diagrams show an increase in the amount of *Betula* pollen and seeds.

The relative pollen values of *Betula* match the regional pollen values (transect group IIa) from present-day *Betula* forests in northern Finland. These data indicate that *Betula* expanded in the valleys. The low NAP values

suggest the existence of a rather dense *Betula* forest.

(b) *Upland*. In the upland diagram (KHV); no assemblage zone could be established since the number of spectra is too small. In these spectra *Betula* pollen reaches values of about 60% and NAP and *Juniperus* about 20%. The pollen concentration values of *Betula* are also high. Almost no macrofossils were observed, except for a few *Betula* seeds.

Surface samples from northern Finland show almost the same regional values for *Betula* in the tundra vegetation. It is likely, therefore, that *Betula* was present. However the NAP values are high, especially *Artemisia*, indicating that the upland vegetation was quite open and steppe-like, rather than a closed forest.

*Pinus* pollen shows very low values (2–8%) both in the oxbow and in the pingo melt hole diagrams, much lower than in the present-day surface samples of the tundra in northern Finland (transect group III). This indicates that *Pinus* was extremely rare or even absent.

#### Phase 3: 11,500–11,000 yr B.P.

(a) *Valley*. The time span of phase 3 is represented by the *Betula Populus* assemblage zone, characterized by pollen values of 60–84% for *Betula*, low NAP values and pollen values of 16–25% for *Pinus*. The distinct rise of the relative *Pinus* pollen values compared with the previous zone is matched in the concentration diagrams. The flood-plain forest consisted of *Betula* and *Populus*, as is testified by the presence of macrofossils of *Betula* seeds and catkin scales of *Populus*. If we compare the relative pollen values of the cores with those from the surface samples in northern Finland, then the best fit is with those from a *Betula* forest with small *Pinus* stands, at distances where *Pinus* shows extra-local values.

(b) *Upland*. The *Betula* NAP assemblage zone is characterized by pollen values of 75–86% for *Betula*, 4–14% NAP and 0.5–5% for *Juniperus*. Also the concentration diagram shows high

pollen concentrations of *Betula* pollen. A few seeds of *Juniperus* and many seeds of *Betula* were found. Clearly, *Betula* was nearby. If we compare the relative pollen values of *Betula* with those from present-day northern Finland, then this assemblage must be interpreted as an open *Betula* forest with *Juniperus*. The open space between the trees was occupied by "steppe" elements such as *Artemisia*, *Anthemis*, *Stellaria media*, etc. The relative pollen values of *Pinus* are low (2–6%) in contrast to the assemblages from flood-plain locations. Also the concentration values are low. This indicates that *Pinus* was absent on the upland. A striking feature is the presence of flowers and leaves of *Erica tetralix*. According to Ellenberg (1978), this species requires a cool summer, a mild winter and an acid soil. This may indicate that the climate to promote the settlement of this taxon had a sufficiently oceanic character for quite some time. On the basis of theoretical considerations, Geel and Kolstrup (1978) accepted that at the beginning of the Allerød the depression tracks began to reach NW Europe, resulting in a moister climate with milder winter temperatures.

The evidence shows that at about 11,500 yr B.P., the later part of the Allerød interstadium, *Pinus* migrated into the valleys. From the relative pollen diagrams one would conclude that *Pinus* and *Betula* were competitors in the vegetation. However, there is no evidence for this in the pollen concentration diagrams. Apparently *Pinus* settled in the valleys without affecting the already existing *Betula* vegetation.

In northern Finland, *Pinus* is generally restricted to the soils which are poor in nutrients. It is possible that *Pinus* was growing in similar habitats in Noord-Brabant. It may have taken advantage of the poor, open sandy areas that were not (yet) occupied by *Betula*.

#### Phase 4: 11,000–10,500 yr B.P. (Fig.15.B)

(a) *Valley*. The stable pollen assemblages from the valley locations indicate that in the valleys there is not much change in the *Betula* forest with small *Pinus* stands.

(b) *Upland*. The relative pollen diagrams of the pingo melt holes show *Betula* pollen values of 45–76% and *Pinus* pollen values of 15–45%. The increase of the relative *Pinus* values is matched in the concentration values, although these values remain rather low (about 1/3 of the concentration of *Betula* pollen).

The proportion *Betula*/*Pinus* is like that in the lowland assemblages from the previous zone, comparable with that in present-day small *Pinus* stands at extra-local distances in a *Betula* forest. The presence of *Pinus* and *Betula* nearby on the upland is confirmed by the presence of well-preserved seeds of these taxa. Again, as in the previous zone, *Erica tetralix* occurred on the upland. In addition, *Arctostaphylos uva-ursi*, seeds of which were observed, and *Calluna* and *Empetrum* were part of the upland vegetation. The relative pollen values of “steppe” elements, such as *Artemisia* have greatly decreased.

The decrease of *Artemisia* values and the continuous presence of pollen of Ericaceae indicate that the steppe matrix of the open *Betula*-*Juniperus* forest had disappeared and was replaced by heather vegetation. The reason for this change is probably a continuing leaching of the soil under rather oceanic climatological conditions.

In the pollen assemblages there is an overall decline of the NAP-values. It is obvious that this does not necessarily mean that the density of the forest declined; pollen of Ericaceae have much lower dispersal capacities than *Artemisia* pollen. The trends in the concentration of pollen values of *Pinus* and *Betula* from the pingo melt hole cores indicate that *Pinus* migrated into the upland without competition from *Betula*. There is even a slight increase in the *Betula* pollen concentration values.

Again thus, like in the valleys during the previous phase 3, *Pinus* migrated into an area without having much effect on the pollen deposition of the already existing vegetation. This is only possible when areas without vegetation are available for colonization or when *Pinus* moved into areas that do not contribute much to the pollen deposition, i.e.,

areas occupied by Ericaceae. The  $^{14}\text{C}$  dates indicate that this phase is the lower part of the Late-Dryas, a period for which it is generally assumed that the climate deteriorated. It is interesting to note that this change in climate did not affect the vegetation in the valley but only the presumably more vulnerable (dry?) vegetation on uplands, especially in the expansion of heather and not in that of *Pinus*.

#### *Phase 5: 10,200–9700 yr B.P.*

(a) *Valley*. The time span of phase 5 in the valley is covered by the *Pinus*-*Populus* assemblage zone. The pollen values of *Pinus* are rather high (50–90%); those of *Betula* decrease (60→6%). The macrofossils include *Betula* seeds and some bud scales of *Populus*.

The relative pollen values of *Pinus* and *Betula*, resemble those of surface samples collected in *Betula* forests at the margin or at some distance (5 m) from small to large *Pinus* stands.

The presence of *Pinus* nearby is confirmed by the ever-increasing concentrations of *Pinus* pollen and the presence of *Pinus* seeds and needles in the deposits. The low NAP values indicate a rather closed forest. Under these conditions, transport of macro-remains of *Pinus* is limited. Also *Betula* was present near the coring site, as shown by the presence of seeds of *Betula*.

The pollen concentrations of *Betula* do not change throughout the zone. The relative *Betula* pollen values decrease thus is not real, but a result of an increasing deposition of *Pinus* pollen grains. At Olland, a different picture emerges. The *Pinus* pollen values are much lower (50–65%) and macrofossils of *Pinus* were not recorded. These features suggest that at Olland, *Pinus* was not close to the sampling site. It is difficult to explain this discrepancy. The pollen concentration diagram of the oxbow cores suggests that *Pinus* and *Betula* were not competitors. Perhaps *Pinus* settled in habitats not occupied by *Betula*, but it is difficult at this time to visualize areas which were not yet forested. The only area available for the colonization of *Pinus* is the terrain that emerges from the process of lake filling. At Olland this process

had not yet advanced to the stage of sedge vegetation as it had at the other lowland sites.

The differences in the *Pinus* pollen values between Olland and the other sites indicate, perhaps, that the new additions in the settlement of *Pinus* occurred especially on peaty soils, in areas where lake filling had created suitable habitats.

(b) *Upland*. No change compared with the previous zone.

*Phase 6: 9500–9000 yr B.P.*

(a) *Valley*. The time span of phase 6 is covered in valley situations by the *Pinus Betula Corylus* assemblage zone, characterized by relative values of *Pinus* of 50–90%. The *Betula* pollen values decrease from 30 to 4%. The high relative pollen values of these two tree taxa, the low NAP values (2–4%) and the presence of *Betula* and *Pinus* seeds indicate that a dense forest of *Pinus* and *Betula* was present around the oxbows. The increase in the pollen values of *Corylus* in the oxbow diagrams indicate that *Corylus* migrated into the valley.

Comparison of the relative pollen values with the pollen values of recent surface samples from northern Finland leads to the conclusion that either a *Pinus* forest with *Betula* stands or a *Betula* forest with *Pinus* stands was present around the oxbow sites. A few macrofossils of *Pinus* were preserved, indicating that it may have been present in the vicinity of the basin. The *Pinus* pollen values are very low in deposits that were laid down at this time in a very large late-glacial lake some 15–45 km from the localities in our area.

This indicates that *Pinus* was certainly not dominant. We assume therefore that the valley vegetation was a *Betula* forest with *Pinus* stands.

(b) *Upland*. On uplands this time span is covered by the *Pinus Empetrum* assemblage zone, with relative pollen values of *Pinus* of 50–75%; those of *Betula* decrease (50→25%) and of *Corylus* only up to 2.5%. The few *Betula* and *Pinus* seeds that have been observed may

indicate that *Pinus* and *Betula* were present. The values for pollen of steppe and heather vegetation remain higher than in valley diagrams, indicating that, despite the expansion of *Pinus*, the forest still must have been rather open.

*Phase 7: 8800–8300 yr B.P.*

(a) *Valley*. In the valley cores this time span is covered by the *Pinus–Pteridium* assemblage zone with relative pollen values of *Pinus* of 25–75%, of *Corylus* of 14–40%, of *Quercus* of 2–20% and of *Betula* of about 5%. *Ulmus* pollen is present with 1–3% and *Pteridium* spores with constant values of about 5%. Considering the increasing amount of *Ulmus* pollen in the oxbow diagrams, it is likely that *Ulmus* migrated into the valley. At this level, the relative pollen values of *Calluna* and *Pteridium* rise. Today, *Calluna vulgaris* and *Pteridium aquilinum* are species that occur in the QUERCION ROBORI PETREAE, forests of base-poor and rather dry soils. It is possible that *Calluna* and *Pteridium* occurred together on the dry sandy base-poor slopes of the valley. Of all the upland elements, seeds of *Betula* and of *Pinus* and needles of *Pinus* were the only macrofossils found in the deposits.

(b) *Upland*. In the upland cores, this time span is represented by the *Pinus–Corylus* assemblage zone, with 45–75% *Pinus* pollen, 5–50% pollen of *Corylus* and NAP values of 1%. The increase in the concentration values of pollen of *Corylus* and the decrease in the concentration of *Betula* pollen at the same level, suggest a replacement of *Betula* by *Corylus*. The concentrations of *Pinus* pollen, however, do not change and remain rather high, again contributing to the notion that *Pinus* did not play a role in the succession on the upland, but had settled in locations where *Corylus* could not germinate, i.e., on peaty soils in the valley. The observation of some seeds and needles of *Pinus* in the pingo melt hole cores indicates that *Pinus* trees were present around the pingo melt hole; however, most of the seeds of *Betula* and seeds and needles of

*Pinus* were found in the oxbow cores, indicating that *Betula* and *Pinus* occurred in the valleys.

This opinion is confirmed by the trends in the pollen concentration curves. The high relative pollen values of *Corylus* and the low NAP suggest a *Corylus* "forest" on the upland, in which other trees did not become abundant.

*Phase 8: 8000–7600 yr B.P.*

(a) *Valley.* The time span of phase 8 is covered by the lowermost part of the *Pinus–Tilia* assemblage zone, characterized by pollen values of 50–75% for *Pinus*, for *Corylus* 12–20%, for *Betula* and *Quercus* about 5–15% and for *Ulmus*, *Tilia* and *Fraxinus* up to 3%. The relative pollen values indicate that *Tilia* settled into the valley. *Tilia* is an entomophilous tree with rather low dispersal capacities (Pohl, 1937); therefore, *Tilia* may have played a more important role in the vegetation than the low relative pollen values would suggest. Nevertheless, the pollen values are too low (much lower than those found in some small basins in the province of Limburg by Janssen, 1960) to suggest that a *Tilia* forest was present as has also been postulated by Iversen (1960, 1964) for Denmark.

Since the *Corylus* pollen values decline at the level where pollen of *Tilia* appears, it is likely that *Tilia* replaced part of the *Corylus* vegetation. Today *Tilia* is a tree of rich, moist soils of the ALNO- PADION (Westhoff and Den Held, 1969). It is unlikely that *Tilia* was growing on the poor acid coversands or in the mire itself. Therefore, the most likely habitat for *Tilia* would be the transition between flood plain and upland. This tallies with Munaut (1967) who found *Tilia* present in the Kempen along the margin of peatbogs.

This opinion is also supported by the contrast in the pollen values in our diagrams: the pollen values of *Tilia* are lower in the upland than in the valley diagrams. Also the *Tilia* pollen shows maximum values in the smaller basins of the valley sites (Olland and Gemonde).

(b) *Upland.* In the upland cores the time span of phase 8 is covered by the *Corylus Pteridium* assemblage zone, with relative pollen values for *Corylus* of 40–60% for *Pinus* of 25–50%, *Betula* of 5–15% and *Ulmus* and *Quercus* up to 5%. *Pteridium* has low pollen values of up to 2%. Macrofossils observed include seeds and needles of *Pinus* and flowers of *Calluna vulgaris* and *Erica tetralix*, pointing towards the presence of a heather vegetation.

Just as in the valley cores, at the level of the empirical limit of *Ulmus* there is an expansion of the values of *Pteridium* spores. However, the relative values of *Pteridium* in the pingo melt hole cores are much lower than those from the valley cores. This may mean that *Pteridium* was most abundant in the valleys despite its preference for drier soils (Watt, 1976). Munaut (1967, Hannappes) concluded from samples taken from a transect from peat to sandy slopes next to the mire, that *Pteridium* was growing on the sandy slopes bordering the mire. Many authors (Godwin, 1956; Smith, 1970; Iversen, 1973; Evans, 1975) connect the expansion of *Corylus* with human activities, i.e., the collection of hazelnuts (Godwin, 1956; Iversen, 1973). In many mesolithic sites from the Boreal, numerous hazelnuts were found (Jenssen, 1953; Clark, 1954). There are some similarities in the assemblages with those during the much later Neolithic landnam, in that in both the pollen values of NAP like *Pteridium*, *Artemisia*, *Plantago lanceolata* and *Polypodium* expand. Especially *Pteridium* expands on sandy soils after interaction by man (Troels-Smith, 1955; Smith, 1970). These features strengthen the notion that the observed changes at the onset of phase 8 have something to do with the activities of man.

An alternative explanation for these phenomena would be to assume changes in the climate. It is difficult, however, to imagine a change of the climate that simultaneously triggered the expansion of a number of ecologically quite different plant taxa such as *Artemisia*, *Corylus*, *Pteridium* and *Ulmus*.

### Summary and concluding remarks

This study shows that the chronological order of appearance of pollen types is similar both in the valley and on the upland, viz., *Betula*, *Pinus*, *Corylus*, *Quercus*, *Ulmus*, *Tilia* and *Alnus*. Also, the sequence of increase and decrease in the values of these pollen types is similar in the diagrams from both localities. However, valley and upland cores differ in the following ways:

(1) *Populus* occurred exclusively in the valleys. *Empetrum*, *Erica tetralix* and *Arctostaphylos uva-ursi* only on the upland.

(2) *Pinus* and later *Tilia* were more important in the valley vegetation than on the uplands. *Juniperus* and *Corylus* occurred principally in upland situations. From these observations and the use of concentration values and recent surface samples from Finland in comparable situations it follows that the vegetational successions in valley and on uplands followed different pathways.

The well-known scheme of the succession of the main trees by Iversen (1960) (*Betula*→*Populus*→*Pinus*→*Corylus*+*Quercus*) can now be refined as follows:

Vegetational succession:

Valley	Upland
<i>Alnus</i> + <i>Tilia</i>	<i>Corylus</i> + <i>Quercus</i> + <i>Ulmus</i>
↑	↑
<i>Pinus</i> + <i>Corylus</i>	<i>Corylus</i> + <i>Quercus</i>
↑	↑
<i>Pinus</i> + <i>Betula</i> + <i>Corylus</i>	<i>Betula</i> + <i>Corylus</i>
↑	↑
<i>Betula</i> + <i>Pinus</i>	<i>Betula</i>
↑	
<i>Betula</i> + <i>Populus</i>	
↑	
<i>Betula</i>	

(3) The  $^{14}\text{C}$  dates indicate that tree taxa immigrated into the upland 300–700 years later than in the valleys, resulting in quite different vegetation types, side by side in almost any segment of the Late Glacial and early Holocene. A “pre-Boreal type of vegeta-

tion” existed in the valley when a “Late Dryas type of vegetation” occurred on uplands and a “pre-Boreal type of vegetation” still lingered on uplands when the valley vegetation was already in the “Boreal” stage.

Much of the establishment of this diversity in the vegetation depends on the reliability of the  $^{14}\text{C}$  dates. In fact, when the diachronous nature of the zone boundaries between an oxbow core (Keldonk) and the pingo melt hole cores became apparent, a second set of  $^{14}\text{C}$  dates was obtained from another oxbow core (Everse Moerkuilen). The results are not different. It is possible that some of the  $^{14}\text{C}$  dates are in error, but not that all the dates within a core are wrong. We assume therefore, for the time being, that the  $^{14}\text{C}$  dates are correct and an indication of a true diversity in the vegetation.

As to the cause of the observed diversity, one can only speculate. It seems unlikely that for a small area such as has been studied in Noord-Brabant, the differences in time are a result of the usual time lag that occurs when a taxon migrates over large distances. In this case, the contrast between upland and valley vegetational successions may be due to edaphic differences, a more fertile and wetter soil in the valley and drier soils, poorer in nutrients, on the uplands.

The resulting vegetation mosaic is what one would expect when species migrate: initial settlement in the most favourable habitats, i.e., the valleys. Today, such a diversity occurs at the margin of the distributional area of plant taxa. However, it must be realized that the distributional limits of many plant species were established after a regressional process, the new limit being determined by the new equilibrium between plant life and climate. In the early Holocene, all migrational processes were progressive and one must contend that many distributional limits at that time were not determined by a climatological parameter, but by the migratorial velocity.

Under these conditions, it is difficult to accept spatial vegetation diversity on the basis of marginal climatological phenomena.



We do not have a ready answer to this problem. It is possible that the environmental differences between valley and upland became more pronounced in the early Holocene because of increasing eutrophication by the rising groundwater table.

At any rate, this study shows that a correlation in time of zones from various site types on the basis of pollen features alone is hazardous: such a correlation may lead to false conclusions on the fine spatial distribution of the vegetation.

Generally, it can be said that a useful correlation of pollen diagrams for the purpose of vegetational reconstruction requires:

(1) a full set of radiocarbon dates in order to establish the ages of the zones independently from the pollen data. The desirability of this procedure was put forwards by Cushing (1967) for regional zones. This study indicates that it is equally important for "local" pollen zones.

(2) information on the size of the basin in order to decide whether the pollen deposition is regional or whether the extra-local component is likely to be important.

(3) information about the site type, upland or lowland.

## References

- Aario, L., 1943. Über die Wald und Klimaentwicklung an der Lappländischen Eismeerküste in Persamo, mit einem Beitrag zur nord- und mitteleuropäischen Klimageschichte. *Ann. Bot. Soc. Zoöl. Bot. Fenn.* "Vanamo", 9: 1-155.
- Benninghoff, W.S., 1962. Calculation of pollen and spores density in sediments by addition of exotic pollen in known quantities. *Pollen Spores*, 4: 332-333.
- Beyerinck, W., 1947. *Zadenatlas der Nederlandse flora*. Veenman, Wageningen, 316 pp.
- Birks, H.H., 1973. Modern macrofossil assemblages in lake sediments in Minnesota. In: H.J.B. Birks and R.G. West (Editors), *Quaternary Plant Ecology*. Blackwell, Oxford, pp.173-191.
- Brooks, D. and Thomas, K.W., 1967. The distribution of pollen grains on microscope slides. 1. The non-randomness of the distribution. *Pollen Spores*, 9: 621-629.
- Clark, J.G.D., 1954. *Excavations at Star Carr*. Cambridge Press, Cambridge, 54 pp.
- Cushing, E.J., 1967. Late-Wisconsin pollen stratigraphy and the glacial sequence in Minnesota. In: E.J. Cushing and H.E. Wright (Editors), *Quaternary Paleocology*. Yale Univ. Press, New Haven and London, pp.59-88.
- De Valk, E.J., 1981. Late Holocene and Present Vegetation of the Kastelberg (Vosges, France). Thesis. Univ. Utrecht, 294 pp.
- Ellenberg, H., 1978. *Vegetation Mitteleuropas mit den Alpen in Ökologischer Sicht*. Ulmer, Stuttgart, pp.372-384.
- Evans, J.G., 1975. *The Environment of Early Man in the British Isles*. Elek, London, 216 pp.
- Faegri, K. and Iversen, J., 1975. *Textbook of Pollen Analysis*. Munksgaard, Copenhagen, 295 pp.
- Firbas, F., 1949. *Spät- und Nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen*. I. Bd.: *Allgemeine Waldgeschichte*. Fischer, Jena, 480 pp.
- Godwin, H., 1956. *The History of the British Flora. A factual Basis for Phytogeography*. Cambridge University Press, Cambridge, 384 pp.
- Hedberg, H.D., 1975. *International Stratigraphic Guide: A Guide to the Stratigraphic Classification, Terminology and Procedure*. International Subcommittee of Stratigraphic Classification (I.S.S.C.). Wiley, New York, N.Y., 187 pp.
- Iversen, J., 1954. The Late Glacial flora of Denmark and its relation to climate and soil. *Dan. Geol. Unders.*, 2: 1-80.
- Iversen, J., 1956. Forest clearance in the stone age. *Sci. Am.*, 194: 36-41.
- Iversen, J., 1960. Problems of the Early Post Glacial forest development in Denmark. *Dan. Geol. Unders.*, IV, 4(3): 1-32.
- Iversen, J., 1964. Plant indicators of climate, soil and other factors during the Quaternary. *Rep. VIth Int. Congr. Quaternary, Warsaw, 1961, Sect. 2: 421-428*.
- Iversen, J., 1973. The development of Denmark's nature since the last Glacial. *Dan. Geol. Unders.*, V, N. 7-C: 1-126.
- Jacobson, G.L., 1979. The palaeoecology of white pine (*Pinus strobus*) in Minnesota. *J. Ecol.*, 67: 697-726.
- Janssen, C.R., 1960. On the late glacial and post glacial vegetation of South Limburg (The Netherlands). *Wentia*, 4: 1-112.
- Janssen, C.R., 1967. A comparison between the recent regional pollen rain and the subrecent vegetation in four major vegetation types in Minnesota (U.S.A.). *Rev. Palaeobot. Palynol.*, 2: 331-342.
- Janssen, C.R., 1972. The palaeoecology of plant communities in the Dommel valley, North Brabant, The Netherlands. *J. Ecol.*, 60: 411-437.
- Janssen, C.R., 1973. Local and regional pollen deposition. In: H.J.B. Birks and R.G. West (Editors), *Quaternary Plant Ecology*. 14th Symp. Br. Ecol. Soc., Cambridge, 1972, pp.31-42.
- Janssen, C.R., 1981. On the reconstruction of past vegetation by pollen analysis; a review. *Proc. IVth Int. Palynol. Conf., Lucknow, C 84(2): 197-210*.
- Janssen, C.R., 1984. Modern pollen assemblages and

- vegetation in the Myrtle Lake peatlands, Minnesota. *Ecol. Monogr.*, 54(2): 213–252.
- Jelgersma, S., 1961. Holocene sea level changes in the Netherlands. *Meded. Geol. Sticht.*, C, 7: 1–100.
- Jenssen, K., 1935. The composition of the forests in Northern Europe in epipalaeolithic time. *K. Dan. Vidensk., Selsk. Biol. Medd.*, 12: 1–64.
- Kalela, A., 1958. Über die Waldvegetationszonen Finnlands. *Bot. Not.*, 9: 1–195.
- Lichti-Federovich, S. and Ritchie, J.C., 1968. Recent pollen assemblages from the Western Interior of Canada. *Rev. Palaeobot. Palynol.*, 7: 297–344.
- Matthew, J., 1969. The assessment of a method for determination of absolute pollen frequencies. *New Phytol.*, 68: 161–166.
- Munaut, A.V., 1967. Recherches paléo-écologique en basse de moyenne Belgique. *Acta Geogr. Lovaniensia*, 6: 1–191.
- Pohl, F., 1937. Die Pollenerzeugung der Windblüter. *Beih. Bot. Zentralbl.*, 56A: 365–470.
- Prentice, I.C., 1978. Modern pollen spectra from lake sediments in Finland and Finnmark, north Norway. *Boreas*, 7: 131–153.
- Smith, A.G., 1970. The influence of Mesolithic and Neolithic man on British vegetation: a discussion. In: D. Walker and R.G. West (Editors), *Studies in the vegetational history of the British Isles*. Cambridge University Press, pp.81–96.
- Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen Spores*, 13(4): 358–361.
- Troels-Smith, J., 1955. Pollenanalytische Untersuchungen zu einigen Schweizerischen Pfahlbauproblemen. *Monogr. Ur- Früh- gesch. Schweiz.*, 2: 11–58.
- Tüxen, R., 1931. Die Grundlagen der Urlandschaftsforschung. *Nachr. Niedersachsens Urgesch.*, 5: 59–106.
- Van Geel, B. and Kolstrup, E., 1978. Tentative explanation of the Late Glacial and Early Holocene climatic changes in north-western Europe. *Geol. Mijnbouw*, 57(1): 87–89.
- Van Leeuwaarden, W., 1982. Palynological and macropalaeobotanical studies in the development of the vegetation mosaic in eastern Noord-Brabant (the Netherlands) during Late Glacial and Early Holocene times. Thesis. Univ. of Utrecht, 167 pp.
- Watt, A.S., 1976. The biology of bracken. *Bot. J. Linn. Soc.*, 73(1–3): 229–233.
- Webb, J. III and McAndrews, J.H., 1976. Corresponding patterns of contemporary pollen and vegetation in central North America. *Geol. Soc. Am. Mem.*, 145: 267–299.
- Westhoff, V. and Den Held, A.J., 1969. *Plantengemeenschappen in Nederland*. Thieme, Zutphen, 324 pp.