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Climatic Variability During the Past Three Million Years, as Indicated by Vegetational Evolution in Northwest Europe and with Emphasis on Data from The Netherlands

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Climatic variability during the past three million years, as indicated by vegetational evolution in northwest Europe and with emphasis on data from The Netherlands

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Temperate and cold stages comparable to those of the last interglacial–glacial have alternated for *ca.* 2.4 Ma, a time-level regarded as the base of the Quaternary. A curve showing climatic fluctuations according to a number of glacials, interglacials, and temperate oscillations of small amplitude or short duration (interstadials) is given, and the value of pollen records in this context is discussed. Because the position of the individual intervals with known vegetational development on the total timescale is controlled by superposition, the lithostratigraphic position of some of them is reviewed.

Basic differences in vegetational evolution between the Tiglian, Waalian, and later interglacials, as well as the extinction of certain trees at around the time of the transition of the Early–Middle Pleistocene, probably indicate lower temperatures during the glacials which have occurred in the past million years.

Although the established record shows some resemblance to the oxygen-isotope curve of the deep sea, precise correlation is not yet possible. A tentative correlation is discussed.

Introduction

The occurrence of climatic fluctuations in the past is no longer disputed, and discussion has shifted to the question of their number and intensity. Palaeontological data which can reflect such variations have been extensively used as a basis for time-stratigraphic subdivisions. Related to the geographical position, such data have been applied to larger areas, in our case northwest Europe. In The Netherlands, the system of subdivision described by van der Vlerk & Florschütz (1950, 1953) incorporated palaeoclimatic interpretation very early on, especially including information provided by pollen analysis as well as other biostratigraphic data. Initially, the number of cold and temperate stages, based mainly on lithostratigraphic data (cf. Penck & Brückner 1909), was restricted, but investigations, especially those based on palynology, of sediments of Early Pleistocene age (Zagwijn 1957) showed an increasing number of warm and cold phases. Since then the number has increased (van der Heide & Zagwijn 1967; Zagwijn 1974, 1985; Zagwijn & Doppert 1978; Zagwijn & de Jong 1984).

Limitations of the basic data

Pollen analysis has contributed substantially to the detection and reconstruction of vegetational variations in the past. This method, which reveals changes in the composition of the pollen content of sediment sequences, provides an impression of the behaviour of the vegetation during the period covering the sediment sequence under investigation. The information is not complete, however, owing mainly to discontinuity of the sedimentation and the fact that only organic material (peat, gyttja) and fine-grained clastic deposits (clay) are appropriate for this type of investigation. Because these materials are not frequently present in the sediment column (mainly composed of sand, gravel, etc.), continuous sections covering more than one interglacial are scarce for the northwestern part of Europe.

Although pollen diagrams may provide information about changes in past vegetation, the evidence is indirect. The same holds for the climate. In this connection mention can be made of the differences in pollen production between plant species, as a result of which the proportions of the pollen of certain plants in sediments are not the same as those of the same plants in the vegetation.

Other factors, too, complicate extrapolation of pollen data from sediments to vegetation and further to climate. For example, both low temperature and drought impede growth of forests. Interpretation of such open vegetation in pollen diagrams is often difficult, because it is not easy to determine whether they are the result of low temperature, a low rate of precipitation, or both. Another factor is the time needed for immigration. After a period of deforestation of an area, a quick rise in temperature will not lead immediately to the restoration of a forest, because immigration of trees takes time. This means that the re-establishment of forests, as indicated by pollen diagrams, occurred later than the actual climatic change. Inferences about climatic changes should therefore be based on increases in the plants already present in the area. From all this it may be concluded that estimates of temperatures during warm intervals give only minimum values.

Changes in soil conditions can also cause vegetational changes that might be erroneously interpreted as climatic changes. The changes in forest composition at the end of an interglacial in northwest Europe are of interest in this context. In this situation, after progressive leaching of the soil, acidiphilous vegetation expands (e.g. spruce in the forest) while moor vegetation and heath replace trees. Such changes can imitate those resulting from deterioration of the climate. However, only careful examination of other plants or other available palaeontological data can provide confirmation. Present northern limits of plant distribution can coincide with certain isotherms, and such data can be used in palaeoclimatic interpretation. A good example is the present northern timberline in northwest Europe, which coincides with the 10 °C mean summer isotherm. This coincidence is very useful for defining the main outlines of the vegetational history of northwest Europe. It remains to be seen, however, whether present limits are in equilibrium with the climate, whether immigration has been completed, or, for instance, whether man has contributed to recent distribution. The limits of distribution may also have been governed by different factors in different areas, and the coincidence with some isotherms may be accidental.

In spite of these major difficulties, vegetational changes reflected by pollen diagrams can, under certain conditions, be shown to indicate changes in temperature. It must be kept in mind, however, that caution is imperative and that the results are approximations: the values are estimates within a few degrees and are only valid for a given amplitude and latitude.

Climatic variations

The last interglacial–glacial (temperate to cold) cycle can serve as a model for vegetational and climatic variability during the Quaternary. Temperate climatic oscillations of small amplitude or short duration, or both, can be called interstadials. However, a clear-cut

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distinction between interstadials and interglacials cannot always be made. In principle, there can be a whole range of amplitudes of such fluctuations. The resolving power of both the method applied and the character of the sediment sequence under investigation determine whether, for instance, intervals of a very small amplitude will be detectable.

Not only the latitude but also the presence of a considerable area of lowlands make northwest Europe a favourable region for registration of vegetational changes in the past. Here the vegetation varies widely during glacials and interglacials, changing from a very open landscape (barren, tundra, park–tundra) during the glacials to complete afforestation with deciduous trees and conifers in the interglacials. Such changes favour the chance of recognizing climatic fluctuations in the pollen rain recorded in pollen diagrams. As an example, figure 1 shows the

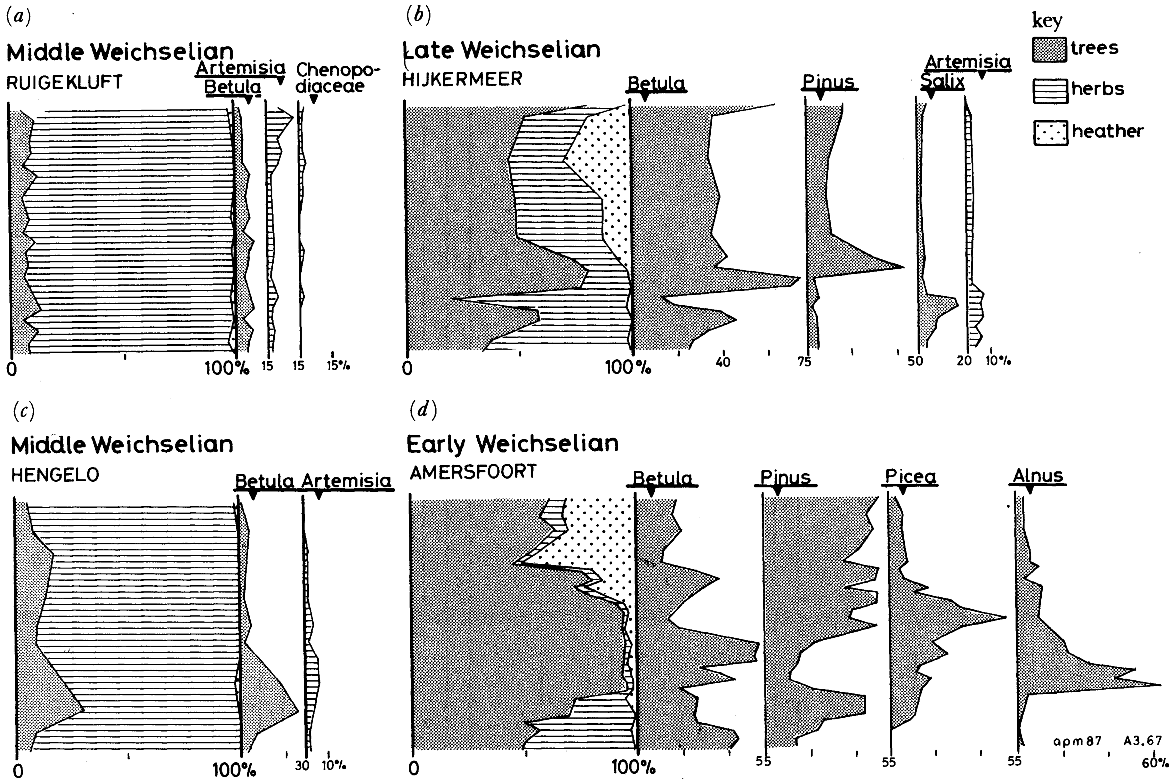

FIGURE 1. Interstadials of the Weichselian cold stage with differences in vegetational development. (*a*, *c*) Hengelo Interstadial of the Middle Weichselian (Zagwijn 1974); (*b*) late glacial with Bølling–Allerød Interstadial of the late Weichselian (van der Hammen 1949); (*d*) Brørup interstadial of the early Weichselian (Zagwijn 1961).

pollen records of four interstadials of the Weichselian, each with a different development of the vegetation. Ruigekluft and Hengelo (figure 1*a*, *c*) (Zagwijn 1974) both represent the Hengelo interstadial of the Middle Weichselian. In Ruigekluft only an increase of herbs already present in the vegetation indicates amelioration of the climate. In Hengelo, dwarf birch in particular increased. Both the diagrams refer roughly to the same period (*ca.* 39 ka BP). Although the differences in the pollen record in these two diagrams may have been caused by a slight difference in age, in which case they would represent different phases in the vegetational development, it is more likely that the variance can be ascribed to different environmental conditions.

The Hijkermeer diagram (figure 1*b*) (van der Hammen 1949) shows a more progressive stage in the vegetational development. In this diagram, characteristic for the late glacial, the vegetational development is demonstrated by the higher values of *Artemisia*, the presence of tree birches, and the appearance of *Pinus* (Bølling–Allerød interstadial). In the upper part of the diagram, further development of forest elements was impeded by the colder climatic conditions prevailing during the subsequent late Dryas stadial.

A still more progressive vegetational development is demonstrated in the Brørup interstadial of the early Weichselian in the Amersfoort region (Zagwijn 1961). Besides *Betula* and *Pinus*, *Picea* and *Alnus* are also represented, with significant values.

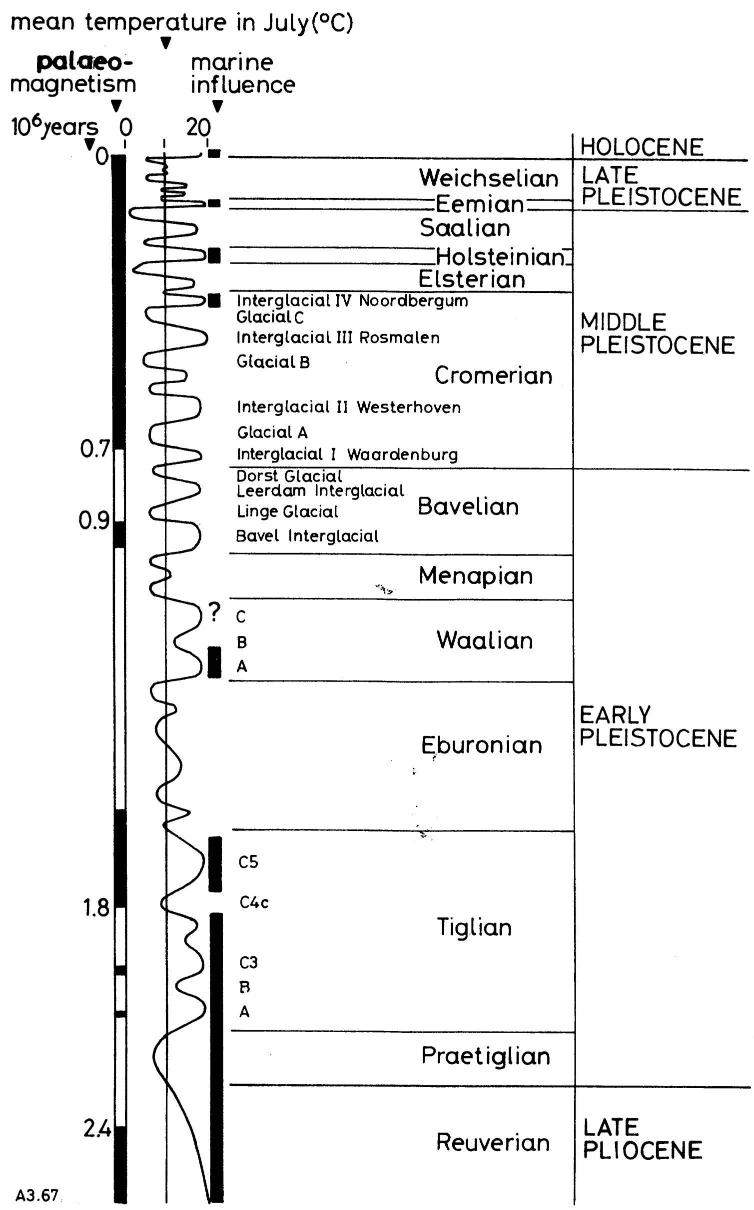

FIGURE 2. Climate curve and chronostratigraphy for the Quaternary of The Netherlands (mainly after Zagwijn 1985).

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Stages: chronostratigraphical subdivisions

Cold phases with a vegetation comparable to that of the last glacial stage have occurred since about 2.4 Ma BP. This time-level is regarded as the base of the Quaternary. In the preceding Pliocene interval there were phases of cooling of the climate but this cooling was less intense than it was after 2.4 Ma BP. Originally there was a tendency to assign stage names, such as Tiglian, Eburonian, Waalian, Menapian and Cromerian, to individual interglacial and glacial climatic phases. However, as more palaeoclimatological data became available, particularly those provided by pollen analysis, it became clear that climatic variation had been even more complicated than formerly envisaged.

Predominantly cold stages, such as the Eburonian and the Menapian, have been found to include some intervals of less intensely cold climate. The Tiglian and Waalian interglacials have proved to be complex, because cool phases and even short cold phases were found to have occurred within these periods. Thus the problem arose as to whether each of these warm or cold fluctuations should be considered an interglacial or glacial stage.

This problem became even more critical when it was found that many more true interglacial and glacial phases must have occurred during the interval between the predominantly cold Menapian stage and the cold Elsterian stage, an interval that was originally thought to represent one interglacial called the Cromerian. As long as the true number of climatic variations of this kind was not known (and this may still be the case) it did not seem possible to introduce new stage-names for any of the already recognized interglacial intervals. Definition of the stage boundaries according to the model provided by Late Pleistocene interglacial–glacial change would only be meaningful if it were known with certainty that no other fluctuations had taken place between a given interglacial stage and a given glacial stage. Furthermore, it was evident that the nomenclature would become more and more complicated and difficult to memorize. This can be judged from the climatic curve for The Netherlands, shown in figure 2.

Stratigraphy

In considering the climatic curve of figure 2, it should be kept in mind that the available information about vegetational developments during the Pleistocene is rather fragmentary. The arrangement of the individual phases with known vegetational records in the overall timescale is determined by stratigraphic superposition. Therefore, data concerning the lithostratigraphic position are indispensable. Some cases for which the lithostratigraphic position is of particular interest for the sequence presented in figure 2 deserve discussion.

The present chronostratigraphic system for the Quaternary of The Netherlands is based on evidence from two different areas (figure 3), the first, for the lower part of the curve, being the Central Graben area in the south, starting with the Praetiglian as the base and ending with the Cromerian. For this area it has recently become clear that a series of deposits belonging pollen-analytically to the Early Pleistocene (and therefore thought to be older than the top of the Menapian) and hitherto partly assigned to the Waalian, are in reality younger because they overlie typical Menapian deposits in the stratotype region, also in the Central Graben. Further studies showed that at least two interglacials and two glacials had occurred within this interval, which is now termed Bavelian. In the Central Graben area the Bavelian beds underly the first interglacial of the Cromerian complex (Zagwijn & de Jong 1984).

FIGURE 3. Topographic map of The Netherlands. Geological features and localities of interest in the present context are indicated.

The second area, the source of the upper part of the curve (figure 4), derives from the northern part of The Netherlands, and the evidence is related to the features of glaciation during the Saalian and the Elsterian. In this area the position of an interglacial phase, called Cromerian IV, is of particular interest. The partly marine beds of this interglacial underly a suite of deposits belonging to the Peelo Formation (figure 5). The Peelo Formation partly fills very deep erosional depressions and often has a characteristic facies, called pottery clay (*potklei*). There can be no doubt that the Peelo Formation is in almost every respect the equivalent of the Lauenburg Clay of northwest Germany, which is Elsterian in age. In both areas these deposits underly Holsteinian interglacial beds as well as Saalian till. At first it was thought that the interglacial at the top of the sequence in the southern part of The Netherlands (Cromerian III; see also de Ridder & Zagwijn (1962) concerning the same interglacial), was identical to the interglacial near the base of the Middle Pleistocene sequence in the northern part of The Netherlands (Cromerian IV), but pollen analysis has shown that this is not the case. For instance, Cromerian IV (figure 6, Roswinkel) has *Abies*, whereas Cromerian III (figure 6, Het Zwinkel) does not; Cromerian III has *Carpinus* early in the interglacial, but Cromerian IV does not; and there are some minor differences as well.

For the northern part of The Netherlands, mention may be made of two interstadials known from the Early Saalian (Hoogeveen and Bantega interstadials) (figure 4). In Bantega (Zagwijn

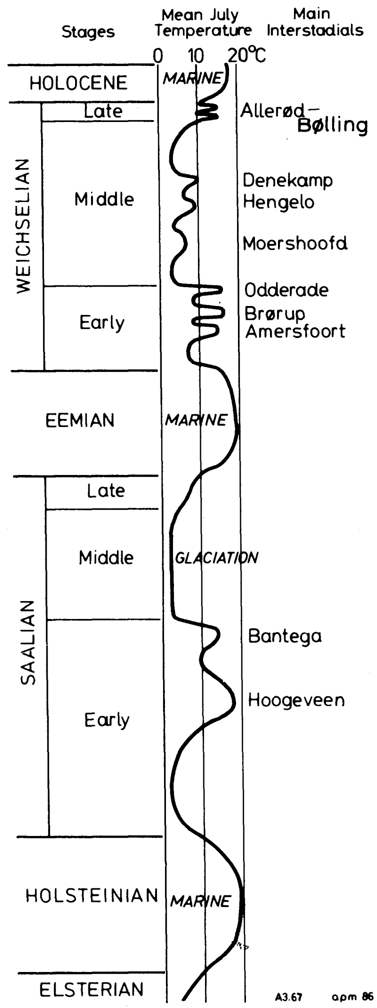

FIGURE 4. Climate curve and chronostratigraphy of the later part of the Quaternary of The Netherlands, based mainly on data for the northern part of The Netherlands.

1973) these interstadials are represented by partly organic beds intercalated in periglacial sediments (Eindhoven Formation), and are underlain by deposits of Holsteinian age and overlain by the Saalian till. The Hoogeveen interstadial in particular shows evidence of rather warm climatic conditions. It seems possible that the vegetational development is not yet completely known. Figure 7 gives a schematic representation of data obtained from various locations. The pollen diagram shows some features known from interglacials at our latitude.

In the southern part of The Netherlands, in the Central Graben area, periglacial deposits with intercalated loam and organic layers (Nuenen Group) overlie fluvial deposits from the river Meuse (Veghel Formation) (figure 8). The latter are partly of Cromerian III age (Het Zwinkel, figure 6).

So far, only fragmentary pollen-analytical information about the deposits of the Nuenen Group has become available. At shallow depths there are organic layers of Eemian age; at the base the deposits are presumably of Elsterian age. A considerable portion of the deposits must be of Saalian age. Although for this sedimentation area, outside the glaciated part of The

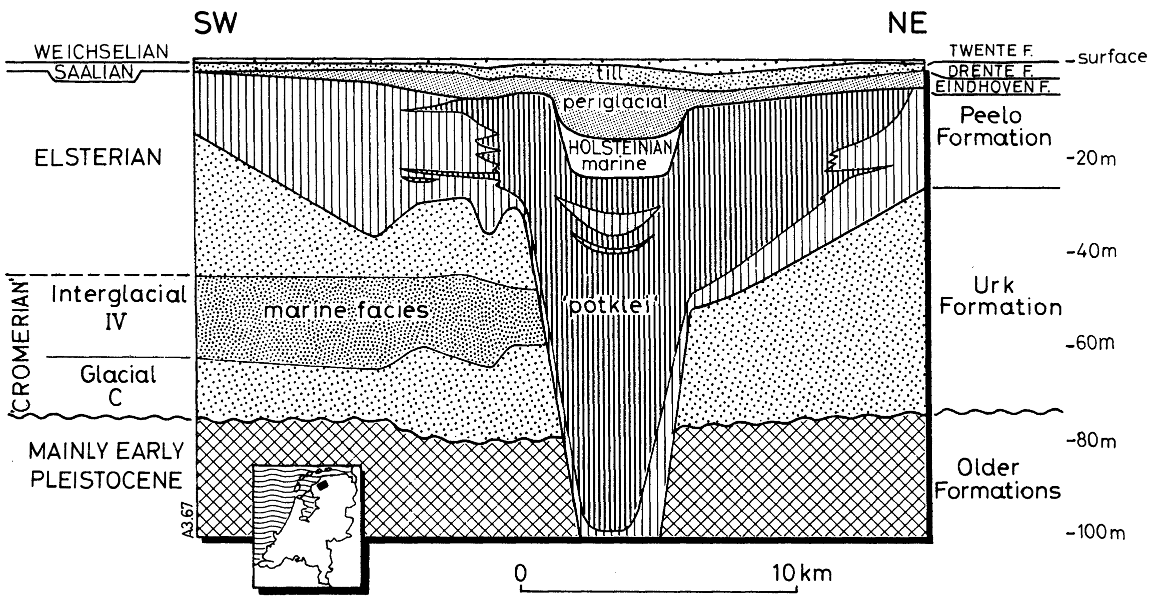

FIGURE 5. Northern part of The Netherlands: section in the Noordbergum area. Modified after Zagwijn and van Staalduinen (1975, p. 17). Peelo Formation composed of fine-grained *potklei* (fine hatching) and more sandy deposits (wide hatching).

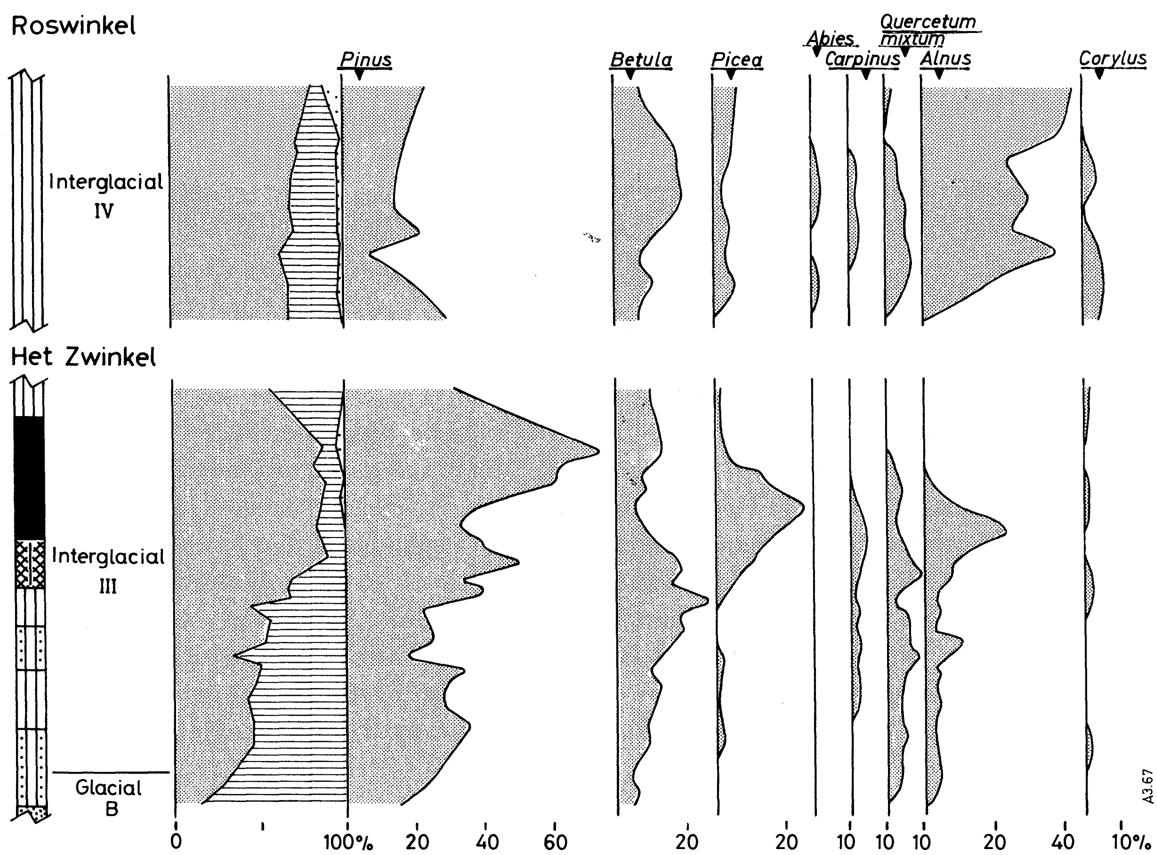

FIGURE 6. Pollen diagrams showing vegetational development in the Cromerian III (Het Zwinkel) and Cromerian IV (Roswinkel) interglacials. (For key to pollen diagrams, see figure 1.) Lithology: hatched, clay and loam; stippled, sand and sandy clay; black, peat with underlying gyttja.

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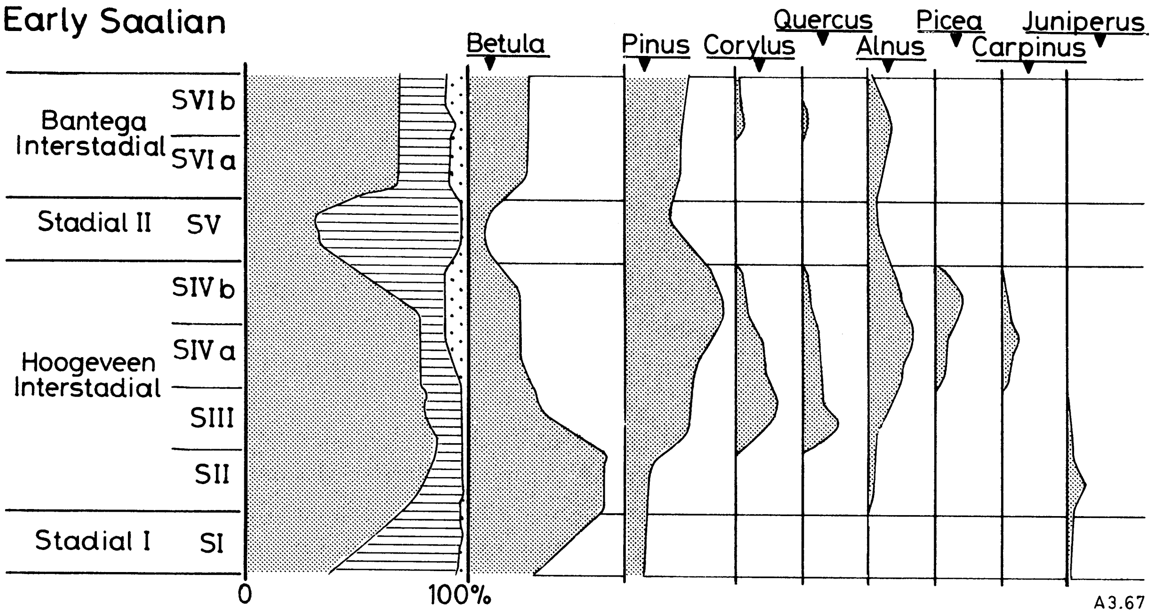

FIGURE 7. Schematic representation of vegetational succession in the Early Saalian, based on data obtained in three localities. (For key to pollen diagram, see figure 1.)

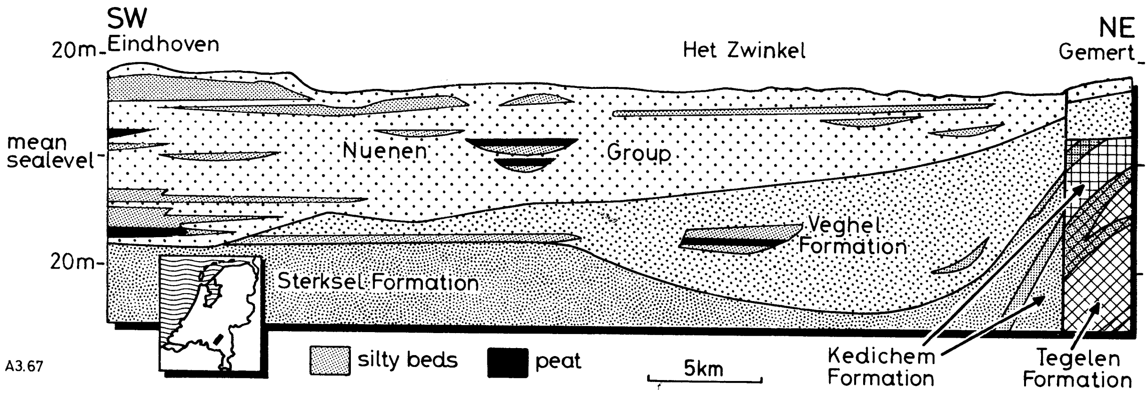

FIGURE 8. Stratigraphic section of the Middle and Late Pleistocene deposits in the Central Graben in the southern part of The Netherlands (modified after Bisschops 1973). Periglacial deposits of the Nuenen Group Overlying fluvial sediment of the Rhine (Sterksel Formation) and Meuse (Veghel Formation). The loamy and organic beds intercalated in the mainly sandy deposits of the latter indicate the position of the Cromerian III interglacial (Het Zwinkel).

Netherlands, rather complete information concerning the development of the Saalian could be expected, the pollen-analytical information is very incomplete. Besides sequences with very open vegetation, there are intervals with a pine-dominated interstadial (Bakel interstadial), presumably correlatable with the Bantega interstadial in the north. There are fragments representing a more temperate interval; these are considered to be parts of an interstadial (Hoogdonk interstadial) which presumably is correlatable with the Hoogeveen interstadial in the north. Just as in the northern part of the country, it is impossible or hardly possible to distinguish short intervals of this interstadial from those of Holsteinian age. In this area the position of the Holsteinian is not definitely known.

Vegetational features

After the Praetiglian cold stage, flora elements characteristic of the Pliocene forest, such as *Sequoia*, *Taxodium*, *Sciadopitys*, *Nyssa* and *Liquidambar*, are no longer present in interglacial floras (Zagwijn 1975), which can be considered as impoverished floras of the Pliocene. Initially some genera still occurred (*Pterocarya*, *Tsuga*, *Carya*, *Eucommia*) which are absent in the recent vegetation as well as during the interglacials of the Middle and Late Pleistocene (the main exceptions being *Eucommia* in the Cromerian I interglacial and *Pterocarya* in the Holsteinian). The transition from the Early to the Middle Pleistocene has been defined on the basis of the occurrence of these 'exotics'. Furthermore, there is a gradual extinction of other elements not restricted to the transition of the Early–Middle Pleistocene (e.g. *Azolla filiculoides*, *Brasenia* (van der Hammen *et al.* 1971)).

A basic difference in the vegetational succession from the Tiglian and Waalian interglacial to the later interglacials is noteworthy. In the younger interglacials the warmth-loving trees show a succession in appearance and maximum distribution (figure 8). This pattern is less distinct during the above-mentioned interglacials of the Early Pleistocene (figure 9); the

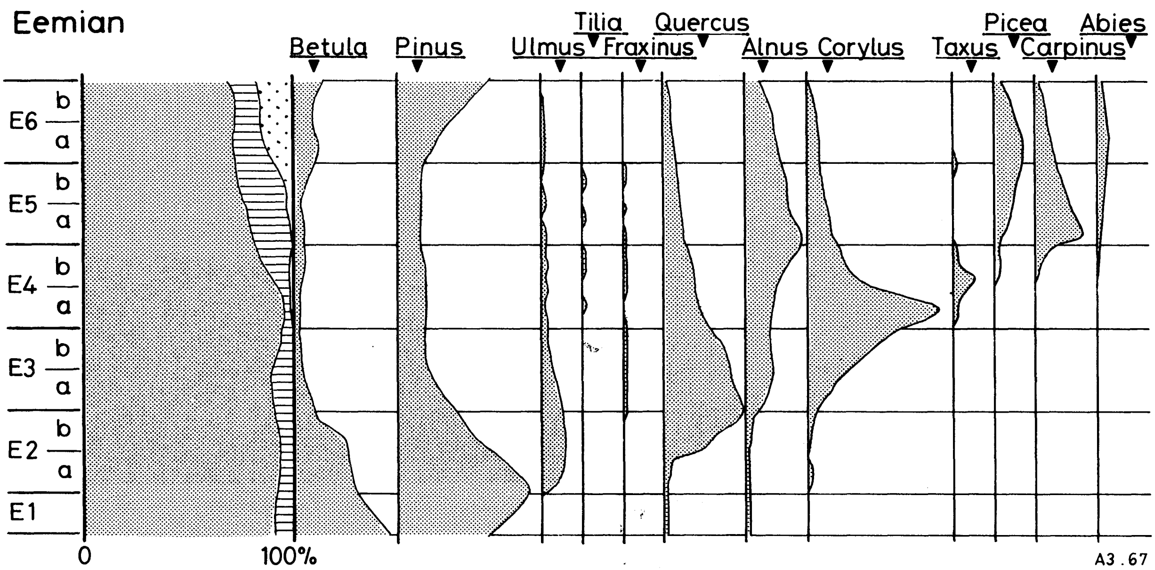

Figure 9. An interglacial of the Late Pleistocene. Schematic example of vegetational development of an interglacial with distinctive evidence for immigration and spreading of trees.

warmth-loving trees seem to spread and decline together. There is no clear succession in the immigration of forest elements, and the majority of the contributors seem to have been present from the very beginning (figure 10).

Besides geological and other conditions, differences in climatic conditions seem to be particularly responsible for this behaviour. Presumably, in this case, the warmth-loving trees did not have to immigrate from a very distant region. This indicates that conditions were less cold in the preceding glacial than during later glacials.

The extinction of the above-mentioned 'exotic' elements in the course of time may also be an indication of increasingly unfavourable climatic conditions in the successive glacials. Most of the genera mentioned now occur in the indigenous floras of North America and Asia under

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climatic conditions which may not necessarily be warmer than the present climate of The Netherlands. Furthermore, they thrive very well in parks in our regions today. It is therefore less probable that the limiting factor was cooler climatic conditions during the interglacials.

To sum up, it can be stated that during the Tiglian and Waalian the extent of the temperate forest was due mainly to climatic amelioration. Immigration seems to have been of less importance and indicates that climatic conditions were less cold in the preceding glacials than in the later part of the Pleistocene. Starting in the Bavelian, the interglacials show a characteristic succession in the appearance and expansion of warmth-loving trees. This indicates a longer immigration distance and therefore presumably colder climatic conditions in the preceding glacial. Most of the exotic elements characteristic of the Early Pleistocene interglacials could, however, maintain themselves up to the Leerdam interglacial, and *Eucommia* was still present in interglacial I of the Cromerian. This may indicate that, during the preceding glacials, these 'exotics' could maintain themselves in Europe and could immigrate once again in the next interglacial. Obviously this was no longer the case during the later glacials of the Middle Pleistocene. These data lead to a general view of increasing colder climatic conditions starting in the glacials from the Early Pleistocene up to those of the Middle Pleistocene.

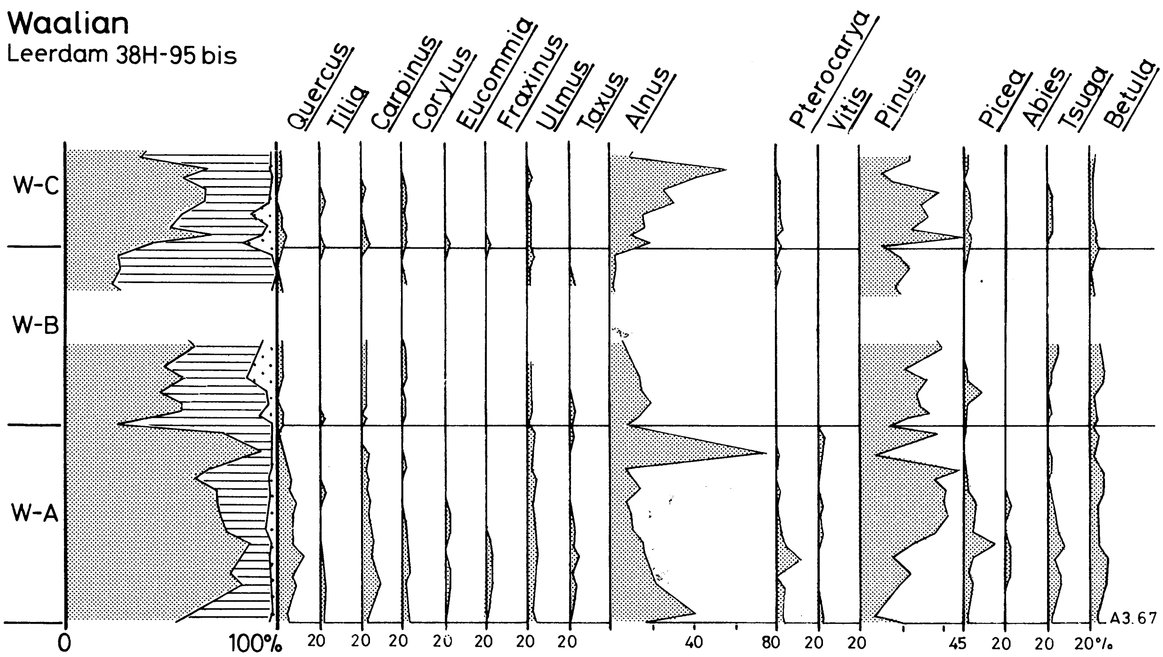

FIGURE 10. An interglacial of the Early Pleistocene. No distinct indications of systematic succession in immigration and culmination of the individual trees (after Zagwijn & de Jong 1984).

MARINE INFLUENCE

During the Neogene, the greater part of The Netherlands was part of the North Sea. At that time, and at the beginning of the Pleistocene, the coastline gradually shifted in the direction of its present position. The first regression away from the position of the recent coastline occurred in subzone TC 4c of the Tiglian. New data (T. Meijer, Geological Survey of The Netherlands, personal communication) show that, in the present coastal area of The

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Netherlands too, marine influence occurs in deposits dating from the later part of the Tiglian (pollen zone TC 5) and from the Waalian (A). For the latter interval, signs of near-coastal conditions were already known (Zagwijn 1974). For the remaining part of the Early Pleistocene and the major part of the Middle Pleistocene in the present coastal area, no marine deposits are known. Starting with interglacial IV of the Cromerian 'complex', the interglacials are characterized again by a marine influence in the present coastal area. Although this behaviour can be ascribed mainly to geological circumstances, there may also have been some influence of climatic conditions.

Correlations with deep-sea isotopic records

The climatic record established for The Netherlands shows some similarities with the oxygen-isotope curve for the deep sea. A detailed correlation with a reasonable degree of certainty cannot yet be made, however. A tentative correlation with core V28-239, originating from the western equatorial Pacific (Shackleton & Opdyke 1976), has been given (figure 11). Although the resolution for the Middle Pleistocene interval is lower in this core than in core V28-238, which originates from the same area, preference is given to the former because the Lower Pleistocene is represented in it. It must be kept in mind, however, that these correlations are tentative and that there are several options.

Concerning the Late Pleistocene, it is generally accepted at present that the Eemian, as represented by its type-site, correlates with stage 5e. Although progress has been made in the application of absolute dating methods (mainly radiometric), the available datings are not yet sufficiently certain to permit general agreement as to the real age of the stages of the Middle Pleistocene. This is especially clear with respect to the position of the Holsteinian, i.e. whether it correlates with stage 7 or stage 9. The rather thermophilous character of the Hoogeveen interstadial and the probable correlation with both the Wacken interglacial (Menke 1968) and the Dömnitz interglacial (Erd 1970; Cepek *et al.* 1981) suggest that they might correlate with isotope stage 7. In this connection reference may also be made to data from Switzerland (Welten, in Schlüchter *et al.* (1985)), where underlying Riss glacial deposits, there are two pollen sequences with an interglacial character. The lower one contains *Pterocarya*, *Abies* and *Fagus* and is very probably correlated with the Holsteinian. The upper one does not have these elements.

The Cromerian IV interglacial beds and lower beds from an earlier glacial period (glacial C) are characterized in the northern part of The Netherlands (figure 2) by the first appearance of the typical volcanic minerals augite and brown hornblende. The influx of these volcanic minerals into the Rhine deposits is associated with eruptions in the Eifel area (Selbergit tuff). Although the lithostratigraphic correlation of the various deposits of the Rhine is complex, radiometric dating of the oldest known Selbergit tuff (Evernden *et al.* 1957; Frechen & Lippolt 1965) points to an age of about 400 ka BP for the first influx of these minerals (Zagwijn 1985). This means that the Cromerian must date from that time or slightly later and can therefore be correlated with isotopic stage 11, in agreement with the estimated date of that stage established by interpolation of the rate of sedimentation (Shackleton & Opdyke 1973).

A series of palaeomagnetic determinations with normal polarity of sediments initially assigned to the Waalian refers instead to deposits of the Bavel interglacial. This leads to the conclusion that palaeomagnetically the Bavel interglacial (base of the Bavelian stage) can be

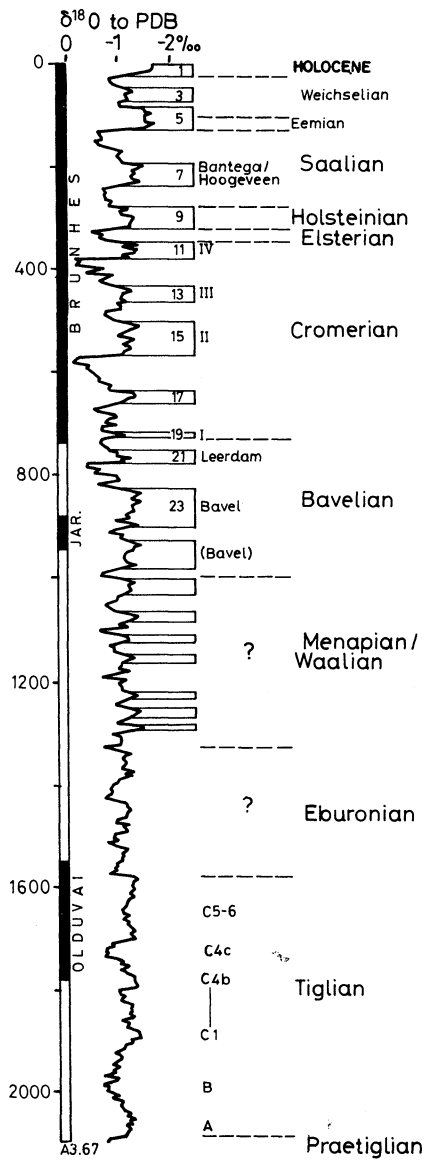

FIGURE 11. Tentative correlation of the climate curve of the Quaternary in The Netherlands with the isotope stages in the deep-sea core V28-239 (from Shackleton & Opdyke 1976).

dated in the Jaramillo (Zagwijn & de Jong 1984). This in turn may point to isotopic stage 23 (25?) for the Bavel interglacial, stage 21 for the Leerdam interglacial, and stage 19 for Cromerian I, because the deposits of the latter two interglacials are palaeomagnetically reversed. Furthermore it is assumed that the amplitude of stage 19 is sufficient for the Cromerian I interglacial. The position of stage 19 in the Matuyama reversed epoch is the case for core V28-238 with a higher resolution, but not for core V28-239.

On the basis of terrace correlations in the Lower Rhine basin in Germany, Cromerian III may correlate with Main terrace 3 (Zagwijn 1985) and could therefore be slightly older than the beginning of the Selbergit volcanism (augite and brown hornblende), that is, slightly older than *ca.* 400 ka. This leads to the suggestion that Cromerian III may correlate with stage 13 and Cromerian II presumably with stage 15, stage 17 in that case representing an unknown, or not accurately classified, interglacial in the continental sequence.

The lower part of the curve permits, on the basis of the position of the Olduvai normal palaeomagnetic interval, a reasonable interpretation for the segment below about 1590 cm, with the Tiglian of The Netherlands. The intervening part, between *ca.* 950 and 1590 cm, shows a considerable number of fluctuations. For this sediment interval, which covers at least the period of the upper part of the Eburonian cold stage, the Waalian interglacial complex, and the Menapian cold stage, a conclusive interpretation does not yet seem possible.

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References

Bisschops, J. H. 1973 *Toelichting bij de geologische kaart van Nederland* 1: 50000. Haarlem: Rijks Geologische Dienst.

Cepek, A. G., Erd, K. & Zwirner, R. 1981 Drei Interglaziale in einer mittel- bis jung pleistozaner Schichtenfolge ostlich von Berlin. *Z. angew. Geologie* **27**, 397–405.

Erd, K. 1970 Pollen-analytical classification of the Middle Pleistocene in the German Democratic Republic. *Palaeogeogr. Palaeoclim. Palaeoecol.* **8**, 129–145.

Evernden, J. F., Curtis, G. H. & Kistler, R. 1957 Potassium argon dating of pleistocene volcanics. *Quaternaria* **4**, 1–5.

Frechen, J. & Lippolt, H. J. 1965 Kalium-Argon-Daten zum Alter des Laacher Vulkanismus, der Rheinterrassen und der Eiszeiten. *Eiszeitalter Gegenw.* **16**, 5–30.

van der Hammen, T. 1949 De Allerød-oscillatie in Nederland. Pollenanalytisch onderzoek van een laatglaciale meerafzetting in Drente. *Proc. K. ned. Akad. Wet.* L**2**, part 1, pp. 69–76; part 2, pp. 169–176.

van der Hammen, T., Wijmstra, T. A. & Zagwijn, W. H. 1971 The floral record of the late Cenozoic of Europe. In *The late Cenozoic glacial ages*, (ed. K. K. Turekan), ch. 15, pp. 391–424. New Haven and London: Yale University Press.

van der Heide, S. & Zagwijn, W. H. 1967 Stratigraphical nomenclature of the Quaternary deposits in The Netherlands. *Meded. geol. Sticht.* **18**, 23–29.

Iversen, J. 1944 *Viscum*, *Hedera* and *Ilex* as climate indicators. *Geol. For. Stockh. Forh.* **66**, 463–483.

Iversen, J. 1954 The late-glacial flora of Denmark and its relation to climate and soil. *Dan. geol. Unders.* **2** (80), 87–119.

Menke, B. 1968 Beitrage zur Biostratigraphie des Mittelpleistozans in Norddeutschland. *Meyniana* **18**, 15–42.

van Montfrans, H. M. 1971 Paleomagnetic dating in the North Sea basin. *Earth planet. Sci. Lett.* **11**, 226–236.

Penck, A., Bruckner, E. 1909 *Die Alpen im Eiszeitalter*, vols 1–3. (1159 pages.) Leipzig:

de Ridder, N. A. & Zagwijn, W. H. 1962 A mixed Rhine–Meuse deposit of Holsteinian age from the south-eastern part of The Netherlands. *Geol. Mijnb.* **41**, 125–130.

Schluchter, Ch., Wegmuller, S. & Welten, M. 1985 *On Quaternary reference sections in the eastern and central Alpine Foreland of Switzerland. Guidebook to the excursions of Oct. 16 and 17, 1985*; *INQUA, Subcommission on European Quaternary Stratigraphy, Symposion, Zurich.* (88 pages.)

Shackleton, N. J. & Opdyke, N. D. 1973 Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes on a 10^5 year and 10^6 year scale. *J. Quat. Res.* **3** (1).

van der Vlerk, I. M. & Florschutz, F. 1950 *Nederland in het IJstijdvak.* (287 pages.) Utrecht: de Haan.

van der Vlerk, I. M. & Florschutz, F. 1953 The palaeontological base of the subdivision of the Pleistocene in The Netherlands. *Verh. K. ned. Akad. Wet.* **20** (2), 1–58.

Zagwijn, W. H. 1957 Vegetation, climate and time-correlations in the Early Pleistocene of Europe. *Geol. Mijnb.* **19**, 233–244.

Zagwijn, W. H. 1961 Vegetation, climate and radiocarbon datings in the Late Pleistocene of the Netherlands. Part I: Eemian and Early Weichselian. *Med. geol. Sticht.*, **14**, 15–45.

Zagwijn, W. H. 1973 Pollenanalytic studies of Holsteinian and Saalian Beds in the northern Netherlands. *Meded. Rijks geol. Dienst* **24**, 139–156.

Zagwijn, W. H. 1974 Vegetation, climate and radiocarbon datings in the Late Pleistocene of the Netherlands. Part II: Middle Weichselian. *Meded. Rijks geol. Dienst* **25** (3), 101–111.

Zagwijn, W. H. 1974 Palaeographic evolution of The Netherlands during the Quaternary. *Geol. Mijnb.* **53** (6), 295–468.

Zagwijn, W. H. 1975 Variation in climate as shown by pollen analyses, especially in the Lower Pleistocene of Europe. In *Ice Ages: ancient and modern*, Geological Journal special issue no. 6 (ed. A. E. Wright & F. Moseley), pp. 137–152. Liverpool: Seel House Press.

Zagwijn, W. H. & van Staalduinen, C. J. (eds) 1975 Toelichting bij geologische overzichtskaarten van Nederland, pp. 109–114. Haarlem: Rijks Geologische Dienst.

Zagwijn, W. H. & Doppert, J. W. C. 1978 Upper Cenozoic of the Southern North Sea Basin: Palaeoclimatic and Palaeogeographic evolution. *Geol. Mijnb.* **57**, 577–598.

Zagwijn, W. H. & de Jong, J. 1984 Die Interglaziale von Bavel und Leerdam und ihre stratigraphische Stellung im niederlandischen Fruh-Pleistozan. *Meded. Rijks geol. Dienst* **37** (3), 155–169.

Zagwijn, W. H. 1985 An outline of the Quaternary stratigraphy of The Netherlands. *Geol. Mijnb.* **64**, 17–24.

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