VEGETATIONAL SUCCESSION, FUNGAL SPORES AND SHORT-TERM CYCLES IN POLLEN DIAGRAMS FROM THE WIETMARSCHER MOOR

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SUMMARY

The present article reports the preliminary results of a pollen-analytical study of some peat sections with very short sample distances. The resulting diagrams may be an aid to a better understanding of the vegetational developments within the peat bog. The importance of Fungi is also discussed and the curves for fungal spores are compared with the peat stratigraphy and vegetational succession. Attention is also paid to cyclic phenomena observed in the diagrams; an approximately 80-years' cycle in the *Alnus* curve seems to be apparent.

1. INTRODUCTION

In the last few years we have carried out, in collaboration with groups of students of the University of Amsterdam, detailed pollen-analytical studies of some peat bogs in the eastern Netherlands and adjacent western Germany, the more particular aims of these studies being the elucidation of the vegetational succession leading to the establishment of actual peat bogs, the assessment of the importance of curves of fungal spores as related to recurrence surface, etc., and the pollen-analytical detection of short-term climatic changes. To this end we used a narrow sampling interval. Samples 1 cm long were cut off from the core, the entire column thus being used up. Apart from the pollen grains, moss and fern spores, fungal spores, Rhizopods, and Algae were counted. For the pollen total of the tree pollen diagram 300 grains were always counted. From another pollen diagram representing the total peat section in approximately the same place where the sections Wietmarscher Moor I and II (see *fig. 1*) have been taken, an average "rate of sedimentation" could be calculated. For the Atlantic and Subatlantic this value was found to be 1 cm in c. 19 years and for the Subboreal 1 cm in 28 years (base of Subatlantic 140 cm, of Subboreal 220 cm, and of Atlantic 350 cm below the surface). The average rate of deposition from the beginning of the Atlantic to the recent time is 1 cm in 22 years. Therefore a value of approximately 1 cm in 20 years seems to be a reasonable average for approximate age calculations (see below).

Hence, "climatic" fluctuations of an order of less than 20 years cannot be detected, but fluctuations of a multiple of 20 years, e.g., of the order of 100 years and more, can usually be discerned. However, it has to be emphasized that this may only be possible in *Sphagnum* bogs, where the disturbing action of

Fig. 1. Location of sections Wietmarscher Moor I and II.

burrowing animals is negligible, whereas in lake sediments the reworking of the sediment by the soil fauna may conceivably render such a narrow sample spacing meaningless.

We soon discovered that vegetational successions could often be clearly recognized, that the percentages of fungal spores showed apparently significant, pronounced fluctuations, and that minor cycles were evident in the curves of several pollen types.

Although these studies are far from concluded and will be continued in the near future, we thought it useful to publish some of the provisional results already. An intensive study of the different spores of Fungi and their vertical distribution in peat bogs is being carried out in our laboratory.

The two diagrams here presented are from the Wietmarscher Moor (Niedersachsen, Western Germany; for its location, see *fig. 1*). Diagram I (*fig. 2*) represents the lowermost metre of the total peat cover of ca. 350 cm thickness and diagram II (*fig. 4*) represents a section covering a more important recurrence surface. We will successively discuss (A) the initial development of the peat bog vegetation, (B) the importance of the Fungi curves as related to the succession below and above a recurrence surface, and (C) the cyclic fluctuations of some pollen curves and their possible explanation.

2. THE POLLEN DIAGRAM WIETMARSCHER MOOR I AND THE INITIAL DEVELOPMENT OF PEAT BOG VEGETATION

The diagram Wietmarscher Moor I (*fig. 2*) represents the lowest metre of the peat, extending from 260 cm to 355 cm below the surface. Two general diagrams were composed, one being a tree-pollen diagram and the other being based on a pollen total including *Betula*, *Pinus*, and the herbaceous pollen. This last diagram is believed to yield some insight into the changes of the bog vegetation only as far as low, open vegetation and stands of forest are concerned. The basic assumption that led to the composition of the pollen total of this last-mentioned diagram is that *Pinus* and *Betula* pollen, besides a relatively low influx from elsewhere, were produced by local stands of these trees on the peat bog itself during the first stages of its development. This assumption is based on the fact that wherever the percentages of *Pinus* and *Betula* pollen rise considerably above the values of 10% and 15%, respectively, in this diagram, also macrofossil remains (wood, twigs, leaves or cones) were found in the sections. The lowermost 5 cm of the section are probably of Boreal, the remaining part of Atlantic age.

The zonation of the diagram and reconstruction of the vegetation

1. For the description of the development of the local type of bog vegetation an arbitrary letter/cipher zonation was applied to the diagram (see *fig. 2*). For a primary zonation with letters the tree pollen diagram was used. Since *Alnus*, *Betula*, and *Pinus* are the more important contribuants to the pollen total, these three elements were chiefly used to make the following division:

Zone A: A marked dominance of *Pinus* with lower *Alnus* and *Betula* percentages.

Zone B: The percentage of *Pinus* decreases and the percentage of *Betula* increases to about 35% of the pollen total, the percentage of *Alnus* initially remaining relatively low but increasing to 30% at the end of this zone.

Zone C: The percentages of *Betula* and of *Pinus* are very low, almost the lowest observed in the diagram. In the upper part of zone C, however, the *Betula* curve rises to 53%. Throughout this zone the percentage of *Alnus* is high, even as high as 70% in the middle of the zone.

The next part of the diagram is rather difficult to subdivide, but on a basis of general trends we may distinguish the next four zones D–G:

Zone D: In this part the pollen sedimentation is characterized by higher *Pinus* and *Alnus* values and a high *Betula* percentage only at the beginning and the end of the zone. The curve of *Pinus* shows a clear maximum at sample number 29.

Zone E: Here we notice a reversed picture in the sense that *Betula* and *Alnus* show comparable values while the *Pinus* curve is considerably lower.

Zone F: This zone is characterized by a somewhat lower *Alnus* percentage and, in the lower part, by a *Betula* maximum of 34% followed by a *Pinus* maximum of 37% (a pine cone was present at this level).

Zone G: The percentage of *Betula* and *Pinus* is very low, that of *Alnus* is high, with an average value of 45%.

By means of this zonation it is possible to describe, in general terms, the development of the local and regional tree cover (see *fig. 4*). In zone A a pine forest was present near the site of our boring. In the next zone (B) this forest developed into a *Pinus-Betula* wood. In zone C, however, the former vegetation type was replaced by an *Alnetum*. The woody vegetation of zone D and E is rather difficult to define but from the rather sharp fluctuations of the tree curves it may be concluded that in this part of the diagram a rather continuously alternating occurrence of *Pinus* and *Betula* in a mosaic pattern with herbaceous vegetation prevailed.

During the deposition of zones F and G this pattern changed into an open vegetation in which *Ericaceae* played an important role. By means of this zonation it is also possible to make some remarks about the development of forest on the sandy soils surrounding the peat bog. Starting from the original pine forest in zone A, the so-called *Quercetum mixtum* increases considerably (representation in the pollen diagram 40% at sample 20). From then onward the *Quercetum mixtum* remains more or less constant. This might mean that the regionally present pine forest was finally replaced by a *Quercetum mixtum*.

As regards zone F, it is not possible to make any definite conclusions concerning the composition of the regional forest outside the bog because of the presence *in situ* of *Pinus* in the bog (cones are found in the sediments).

In zone G a decrease in the *Pinus* and *Quercetum mixtum* percentages and an increase of *Alnus* can be observed in the pollen diagram. This may be due to the absence of local stands of *Betula* and *Pinus* and to a higher groundwater table, resulting in a regional increase of *Alnus* on the lower and richer soils and of a more local increase of *Alnus* in the border vegetation of the peat bog.

2. In order to obtain a more detailed picture of the development of the local peat bog vegetation, diagram Ia (*fig. 2*) was drawn up which, as mentioned in the general remarks, was based on a different pollen total. In this new total only those elements were included that formed part of the local stands of bog vegetation: *Betula*, *Pinus*, and the herbs. This enables us to decide whether the peat bog was covered with trees and shrubs or with a more herbaceous vegetation type. The ferns were excluded from the sum because they formed apparently

part of the undergrowth of the forest cover and were not strictly bound to an open type of vegetation. If in this case a percentage of more than 30–35% of herb pollen is taken as indicative of local open stands of vegetation (based on the comparison of pollen percentages and macro-fossil remains), we may use these values to establish the boundaries for our zonation. In this way the diagram can be divided into 17 zones. At a first glance it becomes clear that during zone I, II, III, IV, VI, VIII, X, XII, XIV, XV, and XVI the local vegetation on the bog was more of a forest (or, alternatively, scrub) type. During the intervals represented by V, VII, IX, XI, XIII, and XVII, a more open vegetation type must have occurred.

A detailed discussion of the zonation and its vegetation (see *fig. 3*) follows below.

During the deposition of zone I the pollen sedimentation was dominated by pine pollen with minor percentages of herbs. At the site of our boring a pine wood was probably present during the interval represented by this part of the diagram. At the transition to zone II an increase of the *Betula* and herbaceous pollen and also a beginning rise of the fern spores can be noticed. During zone II this tendency continues and pollen of *Betula* numerically dominates over that of *Pinus*. A remarkable maximum of the fern spores appears also. We may interpret this as follows: In the pine forest of zone I stands of *Betula* invaded and an undergrowth of ferns developed; in the second part of this zone *Alnus* is also present and plays an increasingly important role in the composition of the forest (see the tree pollen diagram). This change may be ascribed to either a rise of the groundwater table or an improvement of the climate. Since the thermophilous elements, such as *Quercus*, *Tilia*, and *Ulmus*, had hardly become established during the formation of zone I and only started to rise in Zone II, we tend to prefer the second explanation, but a combination of the two causes is also possible.

For zone III the picture suggested by the bog vegetation diagram is somewhat misleading; although *Alnus* probably formed here part of the local vegetation, we had to exclude this tree from the diagram because of the fact that the high percentages especially in the upper part of the diagram may certainly not be attributed to *in situ* presence. During the period represented by zone XVII sometimes a percentage of *Alnus* of 30–50% is found, e.g., when the occurrence of an open vegetation of *Ericaceae* can be deduced from the pollen diagram and also from the presence of fragments of heather branches in the sediment. This clearly demonstrates the appreciable "background effect" of the regional stands of alder. In zone III, however, the *Alnus* percentages in this lower part of the tree pollen diagram are even higher and most probably an *Alnetum* was present on the spot. This is supported by the fact that we found pieces of *Alnus* wood in the peat at this level.

The occurrence of this *Alnetum* shows the still rather eutrophic character of the site and a rise of the groundwater table. According to McVean (1956) the alder can germinate and develop in a permanently wet substratum.

In the last part of this zone the curve of *Betula* starts rising and in the next zone (IV) *Betula* dominates in the pollen spectra, accompanied, at the beginning and the end of the zone, by a top in the *Cyperaceae* curve.

The *Alnetum* of zone III has in this phase of vegetational development apparently changed into a *Betula*-rich variant of the *Alnetum glutinosae*. This may be due to a change in the habitat from a continuously wet one to one that periodically dried out and/or to an acidification of the habitat.

In zone V the pollen sedimentation is characterized by high percentages of herbs and lower percentages of *Betula* and *Pinus*. This is the first time that an open vegetation existed at the site of our section. A glance at the *Betula* and *Pinus* percentages shows that in the lower part of zone V more *Betula* is present, in the upper part, however, more *Pinus* pollen is found. The herbaceous vegetation shows us that this zone can be divided into three subzones, viz.:

a. the upper part of the zone in which a major role is played by *Rumex acetosa*,

b. the rather extensive middle part in which *Equisetum* plays an important role, and

c. one with abundant *Sparganium erectum* pollen and a maximum of the *Gramineae* curve.

In this zone V also, for the first time, indicators of open water were found; compare e.g., in subzone *b* and *c* the first appearance of *Tetrahedron* and in subzone *a* of some *Pediastrum*. Moreover, *Nymphaea* appears for the first time in subzones *b* and *c*. The presence of *Sparganium erectum*, *Typha angustifolia* and *Glyceria* sp. renders it highly probable that zone Va represents an equivalent of the *Glycerio-Sparganion*. This implies a considerable rise in the water level as compared to the preceding *Betuletum* phase.

In subzone Vb a relatively long-lasting phase is present in which *Equisetum* plays an important role. In this period also *Cyperaceae* and *Nymphaea* are present. This might indicate the local presence of a *Magnocaricion*-like vegetation with *Nymphaea* in deeper parts of the immediate surroundings.

In the last subzone, Vc, *Rumex acetosa* and *Galium* were found apart from *Equisetum* and *Cyperaceae*, which also may indicate a *Magnocaricion* type of vegetation.

In zone VI there is a change in pollen sedimentation in this sense that pine and birch pollen are making up 60–70% of the pollen total. We must assume that in this period stands of birch and pine were present in this part of the bog. This phenomenon is not of common occurrence in the Netherlands and W. Germany to-day. In a discussion of the peat bogs of the Russian forest steppes P. YAVCHENKO (1958) described a bog with stands of *Pinus* and *Betula* as a result of a successional development from *Carex lasiocarpa* vegetation.

In the next zone (VII) the pollen total contains more herbs and consequently the occurrence of a more open vegetation seems probable. The most important components are *Cyperaceae*, *Rumex acetosa*, *Equisetum*, *Typha*, and *Menyanthes* with some other characteristic grains, such as *Frangula* and *Urtica*. This list of plants again suggests a *Magnocaricion* vegetation of a type comparable with that of zone Vc. A renewed rise of the water table seems probable.

In zone VIII there is a phase with 70% arboreal pollen the main component of which is pine, the herbs mostly consisting of *Cyperaceae*. In zone VIII *Pinus*, with some *Betula*, must have grown *in situ*.

In the following zone (IX) the pollen sedimentation is dominated by herbs and consequently an open vegetation must again have occurred. This vegetation type, comprising *Cyperaceae*, *Rumex acetosa*, *Cruciferae*, and *Menyanthes*, can also be compared with the *Magnocaricion* discussed before.

Zone X is characterized by a predominance of *Pinus* and *Betula* pollen. In this case the percentages of *Pinus* and *Betula* are mostly equal. Also a remarkably high fern value is present. It may be concluded that a *Pinus-Betula* forest with ferns as undergrowth invaded the bog. The herb vegetation is formed by *Menyanthes*, *Cyperaceae*, *Nymphaea*, and *Galium*. In zone XI a pollen total dominated by herbaceous elements (accounting for 80%) is present. The principal elements are in this case *Cyperaceae*, *Rumex acetosa*, *Menyanthes*, *Utricularia*, and *Hydrocotyle*, which renders the presence of a *Magnocaricion*-like phase very probable.

In zone XII *Betula* is more important than *Pinus* (as it is in the following ones) and the contribution of the herbaceous elements fluctuates between 40–60% instead of between 40–80% as in the preceding part. In the first half of this zone *Pinus* still plays an important role in the pollen total, but in the second half its percentage decreases to 15–20%. The herbaceous components also show a change. Throughout this zone the *Cyperaceae* are represented by relatively low values. *Rumex acetosa* is still present but does not show high peaks as it did in zones VI–XI. *Menyanthes*, *Utricularia*, and *Nymphaea* are present. The *Chenopodiaceae* start here to form a continuous curve and also some *Artemisia* is present. A remarkable maximum of the fern curve is noteworthy throughout this zone.

From the above-mentioned combination of species the development of a *Periclymeno-Betuletum pubescentis*-like association seems probable. Only the part from sample 52–55 shows such elements as *Cyperaceae*, *Menyanthes*, *Utricularia* and *Tetrahedron* which might be indicative of a wetter phase developing in the direction of a *Magnocaricion* as discussed before. Towards the end of zone XII, however, the *Betuletum* is re-established.

In the next zone (XIII) a considerable rise in the herbaceous elements reveals the presence of a more open vegetation type. These elements are *Hydrocotyle*, *Rumex acetosa*, *Sparganium erectum*, *Utricularia*, *Menyanthes*, and *Galium*. The presence of *Hydrocotyle* and *Filices* might also indicate that the former birch forest abruptly changed into an open vegetation type with a water table at least temporarily or locally attaining a level distinctly above the surface of the soil.

In zone XIV the pollen sedimentation is dominated by high percentages of arboreal pollen (mainly *Betula*). The herbaceous components are *Gramineae*, *Cyperaceae*, and *Ranunculaceae* in lower percentages. A continuous *Sphagnum* curve starts from there. We may describe the vegetation type as a *Betuletum* with *Sphagnum* in the undergrowth.

In zone XV more or less equal N.A.P. and A.P. percentages are found. It is difficult to conclude whether we have here a more open birch forest or a denser *Cyperaceae* undergrowth.

Zone XVI shows a sharp rise in the *Pinus* curve. Also a cone was found. This gives the impression that a pine-birch forest became established on the bog, which also means a "drier" environment as compared with the former zone.

Towards the termination of zone XVI the *Ericaceae* curve starts to rise and from then on the pollen diagram assumes a completely different character which continues in the last part of the diagram. In zone XVII the *Pinus* and *Betula* percentages decrease and an entirely open vegetation type must have covered the area. In this vegetation the dominant character of the *Ericaceae* is obvious and also *Sphagnum* must have contributed appreciably. This vegetation type belongs to the *Erico-Sphagnion*. Another noteworthy phenomenon is the "periodicity" in the *Ericaceae* curve as well as in the *Alnus* and *Corylus* curves. This will be discussed below.

3. THE IMPORTANCE OF THE CURVES OF FUNGAL SPORES AS RELATED TO THE SUCCESSION BELOW AND ABOVE A RECURRENCE SURFACE

The generic identification of most fungal spores found in peat or other sediments is extremely difficult. Nevertheless it was noted that the total curve for Fungi spores (expressed as a percentage of the pollen total) shows characteristic fluctuations suggestive of some ecological relation (VAN DER HAMMEN 1954 & 1963; GRAHAM 1962). As far as the Wietmarscher Moor is concerned, it was noted in a diagram of the entire 350 cm of peat (not published here) that the total percentage of fungal spores was extremely high (about 3000 %) in the uppermost samples of the locally desiccated surface and in the samples just below the recurrence surface (see *fig. 4*). The lowest percentage of fungal spores was found in the Younger *Sphagnum* peat above the recurrence surface and in the eutrophic to mesotrophic basal part of the peat. Fluctuating, average percentages of fungal spores were found in the Older *Sphagnum* peat. Accordingly, there seemed to be a logical correlation between the course of the total fungal spore curve and the moist conditions of the growing peat; the percentage is high when local conditions are relatively dry and low when local conditions are relatively wet. If this were always true, the total fungal spore curve would be an excellent indicator of alternatingly wet and dry phases in peat bogs, especially of recurrence horizons. To check this supposition a small section of 40 cm length (approximately 120–160 cm below the surface), taken from a peat profile where the presence of two recurrence surfaces was clearly visible by the characteristic changes in colour, was studied. This section was also analysed by taking samples at 1 cm distance from one another. The age is near the Subboreal-Subatlantic boundary. The resulting diagram (see *fig. 4*) shows an obvious correlation between the maximum values of the *Fungi* curve and the relative degree of humification or, respectively, moist conditions at the time of deposition.

In a separate, parallel diagram (*fig. 4*, at the right) the changes of peat bog vegetation are demonstrated by the sum of the pollen percentages of *Gramineae*, *Cyperaceae*, *Ericaceae*, and *Sphagnum*. This diagram seems to confirm that the *Fungi* curve may be of considerable interest for the reconstruction and succession of former peat bog vegetations, especially as an indicator of certain soil moisture changes. The *Fungi* curve in the eutrophic to mesotrophic part of the peat bog (*fig. 2*) is more irregular, the percentages remaining relatively lower (10–600%). However, there also seems to be a certain relation here between the local vegetation and soil moisture or the *Fungi* percentage, respectively. A further study of these phenomena seemed justified and is now being carried out in our laboratory. The fourth author has so far distinguished and counted more than 30 different types, most of them giving very surprising and apparently meaningful curves. Although the taxonomic identification of the different types is a very difficult task, a number of them have already been recognized.

4. CYCLIC FLUCTUATIONS OF SOME POLLEN CURVES IN THE DIAGRAMS WIETMARSCHER MOOR I AND II

In the "centimetre diagrams" of the Wietmarscher Moor (*figs. 2* and *4*) some curves show cyclic fluctuations. The most prominent cyclic fluctuations are present in the *Alnus* curve. In the upper part of diagram I (between sample 73 and 94) these fluctuations start regularly, when the local influence of *Betula* and *Pinus* stands ceases and true *Sphagnum* bog vegetation without trees develops. The *Alnus* curve shows in this interval 5 maxima and 5 minima, every cycle being substantiated by about 5 different spectra. The average "thickness" of the peat corresponding to one cycle is 4 cm. Similar cycles, although partly somewhat less regular, are evident in diagram II. Here also one cycle corresponds with 4 cm of peat. In many cases the maxima of the *Alnus* cycles correlate with minima of the *Corylus* curve. If we take into account the "rate of sedimentation" for the Wietmarscher Moor peat at the place where the sections were taken (about 1 cm in 20 years, see introduction), the average duration of the cycles seems to have been of the order of 80 years (VAN DER HAMMEN, 1969). In this case again more work will have to be done to establish with more certainty the general occurrence of these cycles and to discover their nature. However, a possible explanation might be that climatically determined, slight fluctuations of the water table caused considerable changes in the extension of associations of the *Alnion glutinosae* and *Alno-Padion*, that must have been common in the surrounding area. These fluctuations of the water table could be responsible for two effects which could explain the 80 years' cycle in the curves:

a. a change in the actual composition of the forest, in the case under discussion a replacement of *Alnus* by *Corylus* or *vice versa*; and
b. a change in the phenology of the species concerned, leading to variations in pollen production only, so that possibly only a rather insignificant replacement of trees took place.

At any rate, the occurrence of a climatic cyclic influence of the order of 80 years would not be unlikely, considering that a solar cycle of that length (and its influence on climate and weather) is relatively well-known. It is interesting to note that recently DANSGAARD *et al.* (1971) reported a manifest 78-year cycle of the average temperature, deduced from oxygen isotope studies of a Greenland ice core. Further studies are now being carried out in various peat bogs to find further evidence from pollen diagrams. Cyclic fluctuations are present in some other curves; we may refer here to the diagrams and only draw the attention to the *Ericaceae* curve of the upper part of diagram I, where about three cycles seem to be present. They could be of the order of 80 to 100 years and the explanation could be sought in the cyclic succession of peat bog vegetation (the alternation of a "tussock" and a "pool" community) or in direct climatic factors. However, in this case the evidence from only three "cycles" is certainly not sufficient to establish the occurrence of continuous cyclic regularities.

5. CONCLUSIONS

From the data obtained during our palynological studies the conclusion can be drawn that "centimetre diagrams" of peat bogs may provide the clue to many problems of vegetational succession in time, of minor climatic fluctuations and similar processes. Unfortunately the construction of this type of diagram is very time-consuming. We believe, however, that it is worth-while and may be the only way to achieve any appreciable advances in the study of Holocene vegetation and climate. The analysis of fungal spores may contribute increasingly to this study. The recognition of possible cyclic phenomena may also provide a lead.

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Fig. 2. Pollen diagram of section Wietmarscher Moor I; depth 260–355 cm below surface.

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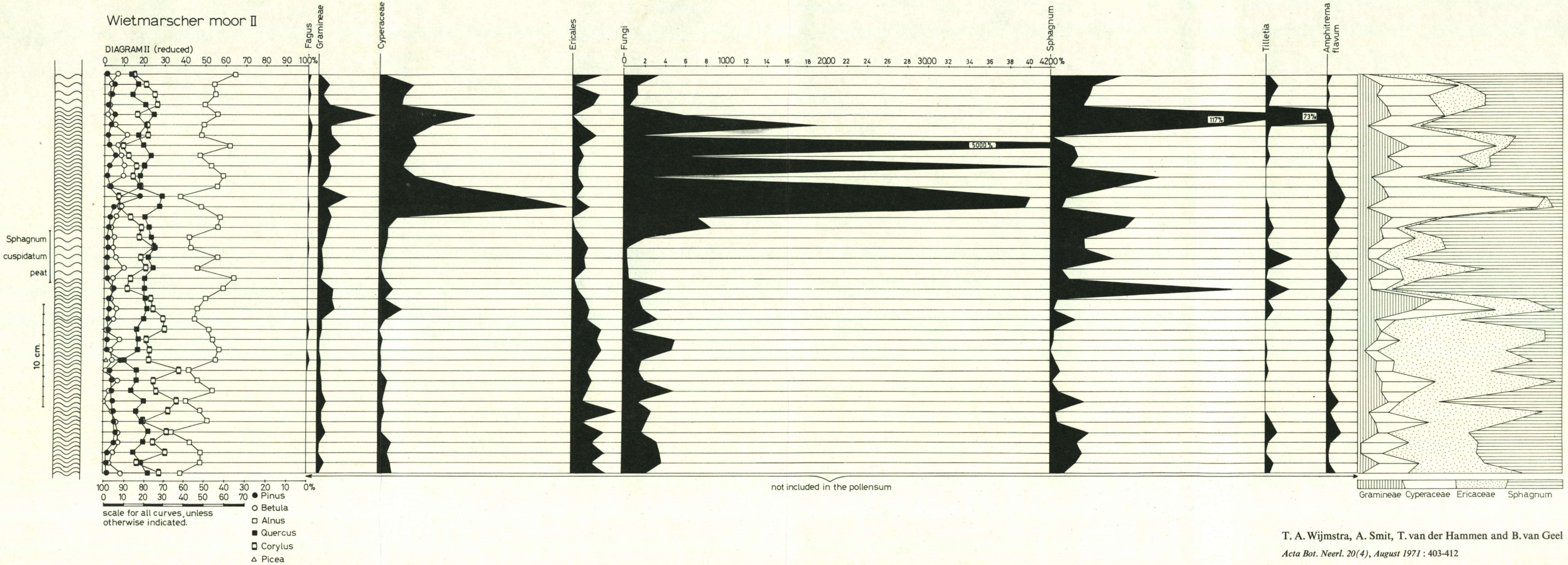

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Fig. 3. Tentative translation of pollen data (diagram Wietmarscher Moor I) into local succession of vegetation types.