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ECOLOGICAL STUDIES OF PEAT-BOG VEGETATION IN THE NORTH-WESTERN PART OF THE PROVINCE OF OVERIJSEL (THE NETHERLANDS)

(PRELIMINARY REPORT)

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ABSTRACT

In the marshy fen country of N.W. Overijsel the hydroseres have been studied ecologically. Several successional sequences could be discerned, which develop as more or less independent and parallel series, but are cross-connected by a continuous range of intermediate and transitional types of vegetation.

In the diagram of these hydroseres the vertical direction from top to bottom represents the progressive succession, and the direction from left to right the increase in the degree of trophism and of various forms of disturbance and interference such as dunging and pollution.

The ecological conditions prevailing in the successive stages of each hydrosere are described, much importance being attributed to the local fluctuations of certain environmental factors. This was substantiated by repeatedly taking water samples in the same spot during the course of the growing season. In many cases the maximum and minimum values of the range are of much greater significance than the average value. In this connection several species of bryophytes are valuable indicators.

In the seres within the area under investigation, and more manifestly so in seres in other parts of Europe (including those occurring in more alkaline situations), several vicarious species (*e.g.*, species of *Drepanocladus, Campylium, Riccardia, Pellia, Calliergon, Mnium, Bryum, Sphagnum, Eriophorum, Carex, Dactylorchis and Salix*) can be recognised in the comparable phases of the hydrosere.

Special attention is focussed on phenomena associated with seepage and their striking effects on the vegetation.

1. INTRODUCTION

A few centuries ago that part of the Netherlands which is referred to in a phytogeographical sense as the "Hafdistrict", *i.e.* Haff or Lagoon District (VAN SOEST in HEUKELS & VAN OOSTSTROOM, 1962), and in which at present so many of the land reclamations ("*polders*") are situated, must have abounded in marshy areas. This "Hafdistrict" includes a considerable part of the western and north-eastern Netherlands. Since the Middle Ages peat was cut in the peat-bog areas of this district. These old peat digging regions have a character of their own, which is brought about, among other things, by the variation of larger and smaller lakes and artificial water ways, by the particular structure of the landscape with its regular alternation of dug-over and of unexploited zones, by a typical hygrosere with a specific flora and fauna, by the ribbon development of towns and villages, by the frequent use of water-carriage, and by a special social structure of the areas under discussion. Such peat bog regions occur throughout the north-western European plains, extending from N. W. France to the Baltic, with an outlying area in East Anglia (England). In the Netherlands the characteristic vegetation types are relatively well developed, and they have been more or less thoroughly investigated especially in the so-called "Vechtplassengebied" (the lake district in the area of the river Vecht; see WESTHOFF, 1949; MEYER & DE WIT, 1955). Undoubtedly the best developed examples are the hydroseres in N.W. Overijsel. The studies undertaken in this area were, up to a few years ago, of a rather incidental nature (VAN DIJK & WESTHOFF, 1955; KUIPER & SEGAL, 1955; KUIPER, 1958). In the last few years a more exhaustive analysis of the ecology of water and marsh vegetations and of its successions was started. So far five students of the University of Amsterdam have participated in this project. The ecological investigations in this region, which is structurally complicated and so rich in species, will require many years to come. Therefore, the following survey can only touch upon those aspects of our field and laboratory studies which now necessitate an extended research programme.

2. TOPOGRAPHY, LANDSCAPE AND HISTORY

The moorland country in N.W. Overijsel covers only a fraction of a large stretch of country moulded by peat digging, which must have extended from Staphorst and Hasselt to well inside the province of Friesland. As is the case with the Vechtplassen area, the hydrology is influenced by the proximity of higher diluvial ground, one of the results being the effect of percolation phenomena on the vegetation (HAVINGA, 1956). This is of essential importance in connection with the understanding of the chemical environmental factors.

The peat moors are situated between the diluvial deposits of Drente (which have an extension towards Oldemarkt), the diluvial high ground of Vollenhove, and parts of the Hafdistrict which in this area border upon the IJselmeer. They constitute the drainage area of the adjoining diluvial regions. The cover sand of Drente, with its series of sandy ridges running more or less in an E.-W. direction, shelves away to the W. and lies below the ground water level near Hasselt, Staphorst, Meppel, Steenwijk and Oldemarkt. Locally the sand lies even at a depth of 3 metres below the water level. Here and there the sand ridges can be traced under the moorland, for instance in the vicinity of Hogeweg (Oldemarkt) and Dwarsgracht (Giethoorn), and at Belt-Schutsloot the cover sand even reaches the surface.

The initial development of the peat deposits took place in the Boreal (EDELMAN, 1950), the accumulation of the peat continuing till several centuries after the beginning of our era. In the period before peat digging commenced, a span of about 1.000 years, the vegetation was

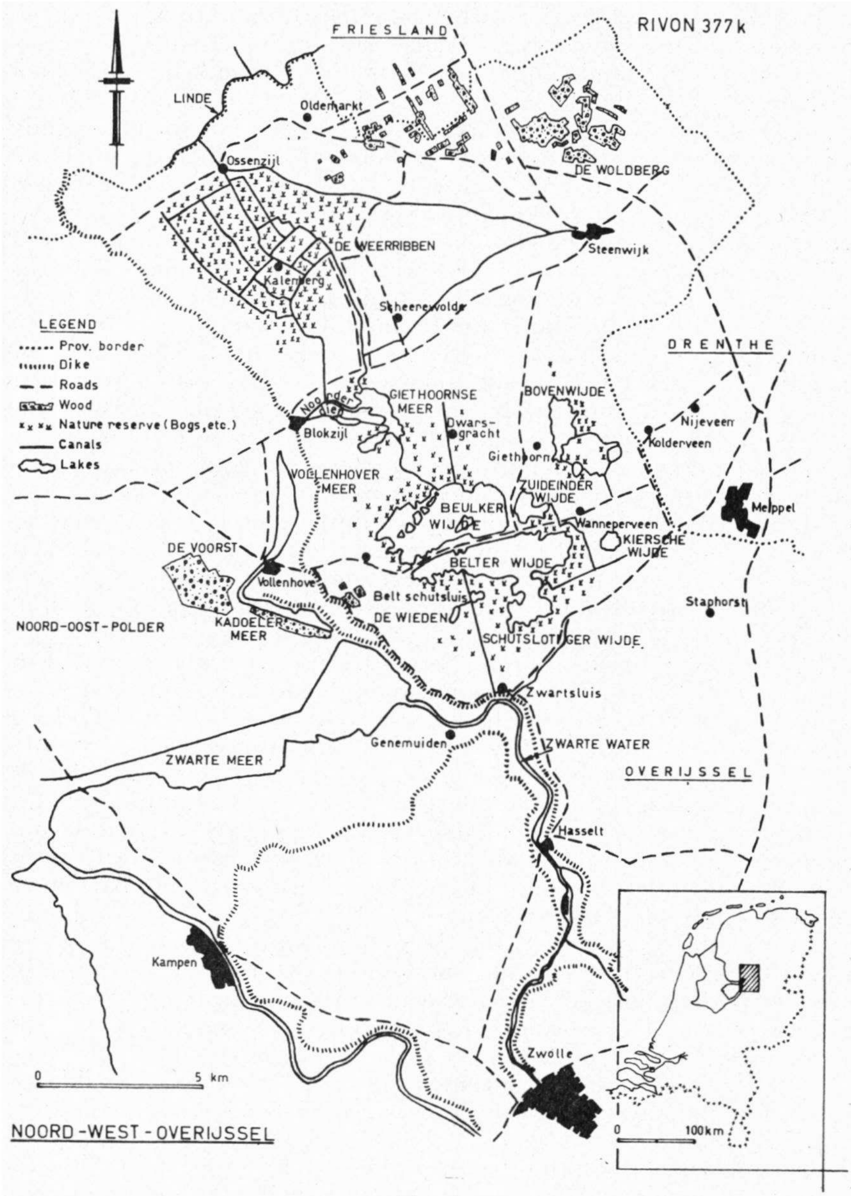

Fig. 1.

presumably in the state of a relative equilibrium, periodic flooding and other natural disasters most probably resulting in a cyclic succession.

Of the original peat-bog region substantial portions have been reclaimed in this century, so that it has now become broken up into several disconnected areas, of which the most important ones are the zones around the larger lakes: Beulakerwijde, Belterwijde, Schutslotigerwijde, Zuideindigerwijde, Bovenwijde en Kierse Wijde (in which a number of smaller lakes are situated), and the country around Kalenberg. The Giethoorn Lake is the oldest. The Beulakerwijde originated through the action of a flood after a dike-burst of the late Zuiderzee in 1825, after which the village of Beulake appeared to have completely been washed away, and other villages, such as Wanneperveen, had to be "shifted" eastwards when they were rebuilt. All other larger areas of open water were formed after injudicious peat digging, the undug balks, which provided approaches to the peat-holes—actually nothing but strips of unsolid peat-moor—having been made too narrow and having become a victim of the wash of the waves. The depth of the lakes hardly anywhere exceeds 2 metres, the peat lying on the sandy subsoil. The alternation of long and narrow peat holes (with their hydroseres) and the approaches (also used as drying fields for the dug peat) is highly characteristic. The combined approach and drying strips, or balks, locally called "*legakkers*" or "*ribben*", used to be covered with a strikingly beautiful vegetation rich in showy flowers, which is typical of the unmanured hay fields, the so-called *Cirsieto-Molinietum*. Nowadays this vegetation type has nearly everywhere disappeared from the legakkers after the regular application of fertilisers.

Landscape and vegetation in N.W. Overijsel are extremely varied. This variation is, to a large extent, undoubtedly the result of human activities. Apart from peat digging the harvesting (cutting) of reed and of rushes is, or was, of considerable importance, whilst hay and other vegetable litter provide materials for cattle farming and horticulture. The reed from N.W. Overijsel is of outstanding quality and particularly suitable for thatching. However, the reed culture is up against some difficulties which have as yet not satisfactorily been solved. One should attempt to stabilize ("freeze") that particular phase or stage of the succession in which the reed produces an optimum yield, and this may conceivably be achieved by a regulation of the water level. The answer to the question in which way this control of the water level must be carried out in practice, can possibly be provided by an ecological study of the natural succession (SCHROEVERS & SEGAL, 1962).

By far the largest area in this moorland region is only attainable by boat, although after the world wars road communication has considerably been improved.

Peat cutting is now a thing of the past, peat exploitation in this area being uneconomical. After the Middle Ages, when the *Sphagnum* peat was dug away, secundary bog-peat accumulated, which was mainly built up by the remains of sedges.

An important factor in moulding the landscape was undoubtedly the varying water level, the changes in the past sometimes exceeding 1 metre. Such extreme variations ceased to exist after the introduction in 1928 of drainage by means of mills and pump installations.

The drainage has without a doubt had a considerable effect on the composition of the vegetation cover, but reliable sources of information concerning the older period are almost entirely lacking.

3. Materials and methods

The phytosociological analysis was carried out according to Braun-Blanquet (1928, 1951); quantitative data of the vegetation records were used to a relatively large extent apart from the qualitative ones, however. The modified Braun-Blanquet scale of Segal & Barkman (1960; see Barkman, Doing & Segal, 1964) for the estimation of abundance and percentage of cover was employed. In this new scale the criteria are judged by objective standards. So far more than 1.000 vegetation analyses have been recorded in the area. For a comparison a few hundred more were recorded in other peat moors and marshy regions in the Netherlands, England (East Anglia), Belgium (Haute Semois), France (Hautes Alpes), W. Germany (Eifel), N. Poland and S. Sweden. It was tried to obtain as much insight as possible into the succession both by a study of the zonation and by the periodical recording of data from 50 permanent experimental plots selected in 1956. Vegetation mapping of a number of sites proved to yield valuable information. For the analysis of the vegetation itself, several factors were taken into consideration apart from abundance and percentage of cover, such as sociability, vitality and fertility. The growth rate of helophyte populations was estimated by recording the height and the number of shoots for a number of years. A considerable number of ecological factors was measured in the field. The exposure was estimated in the larger lakes, and invariably the depth to the mineral subsoil, the thickness of the humus layer, and the water table were measured. In addition, a large number of pH-recordings were made, records being taken repeatedly in the same place throughout the year. Incidental recordings of temperature, relative humidity, wind velocity, the dash of the waves, and light intensity were carried out. A total of about 150 water samples from N.W. Overijsel and another 70 examples from different parts of the *Hafdistrict* were analysed for: specific conductivity ($\varkappa_{18}$), pH, potassium permanganate consumption (filtered and unfiltered), chloride, phosphate, nitrite, nitrate, organic nitrogen, ammonium, iron, calcium, magnesium (calculated), sodium bicarbonate, bicarbonate hardness, and total hardness, and in a number of cases also sulphate, manganese, and the colour according to Hazen.[1]) Sulphide could be demonstrated in a number of cases by the characteristic smell. In seven of the water samples separate estimations were made of total nitrogen in unfiltered and filtered water, and of ammonium and organic nitrogen.[2])

[1]) The chemical water analyses were mostly carried out by the Waterleiding-laboratorium Midden-Nederland at Bilthoven.

[2]) The nitrogen estimations were carried out by the laboratory of the Biological division of the IJselmeerpolders at Kampen.

In 14 localities soil samples were taken, of which pH-H_2O, pH-KCl, and the amounts of calcium, carbonate, humus, total phosphorus, total nitrogen, chloride, and carbon content were measured[3]). In addition, silt analyses[4]) of a few samples from the Netherlands and from abroad were carried out, calcium, magnesium, sodium, potassium, phosphor, nitrogen and silica being estimated.[5])

The various methods of chemical analysis will not be discussed here, a number of methods are dealt with in SNEL (1964) and SEGAL (1965).

Special attention is being paid to the *periodic variation* in a number of chemical and physico-chemical environmental factors, more particularly to the local maxima and minima. These extreme values have, to my mind, an essential bearing on the composition, development and ecology of the vegetation cover.

4. HYDROSERES

4.1. *Literature survey*

The first more comprehensive study of peat and marsh vegetations in N.W. Overijsel was carried out by a group of students of the University of Amsterdam (MEIJER, 1950; DE WIT, 1951). In the years after 1953 the investigations covered more ground and they became intensified (VAN DIJK & WESTHOFF, 1955; KUIPER & SEGAL, 1955; KUIPER 1956, 1958). The survey given by Kuiper (1958) of the state of our knowledge at that time, is the outcome of researches carried out during a few summer months. After 1957 a more intensive study was made during a number of successive summer seasons, which has increased our insight into several problems appreciably.

Kuiper distinguished three independent seres in a fairly eutrophic environment, and two eutrophic seres. The seres in a seepage area are characterised by the "*Caricetum diandrae*", the "*Phragmiteto-Caricetum lasiocarpae*" and the "*Menyantheto-Juncetum subnodulosi*", respectively, which associations, following VANDEN BERGHEN (1952), are all divided in a *Scorpidium-phase* and a *Sphagnum*-phase, the first preceding the latter in the succession. According to Kuiper the seres in eutrophic water are characterised by the "*Thelypterideto-Phragmitetum*" and the "*Magnocaricetum*". The last is a collective name for vegetations in which *Carex acutiformis*, *C. paniculata*, *C. riparia*, *C. vesicaria* or *C. acuta* occur. (The last two species do not appear in hydroseres in peat-moor country, however). The first four seres were supposed ultimately to develop into the "*Cirsieto-Molinietum*" or into *Sphagnion fusci* vegetations, the last-mentioned sere into the *Thelypterideto-Alnetum*.

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3) Soil samples were tested by Biologisch Station Weever's Duin at Oostvoorne.
4) Silt analyses were carried out by the Institute of Physical Geography at Amsterdam.
5) Ash analyses of plant material were carried out by the Royal Institute for the Tropics at Amsterdam.

4.2. *A succession diagram*

The investigation has shown that the successions can not be described in terms of simple schemes. The number of possibilities, partly on account of various cultural influences, is legion, and numerous seres are connected by transitional stages. The scheme provided in fig. 2 is a simplified diagram of the hydrosere in N.W. Overijsel. Taking this diagram as our starting point, several aspects of the succession will be explained.

It must be pointed out at the onset that the succession of marsh vegetations cannot be satisfactorily represented in the form of a two-dimensional diagram. If one intends to indicate the direction of the succession on the one hand (inclusive of degeneration and regression phenomena), and wishes to emphasise the effect of ecological factors on the other, this appears to be impossible if a single master factor can not be held responsible for the differences in the developmental series of the succession. In the succession itself, gradients can simultaneously be indicated for both the accumulation of humus and the water table, with which peat consistency and eutrophism of the water are also correlated. Particularly as a result of the local agricultural practice of reed and hay cutting which gradually deplete the substratum of essential mineral constituents, the ion concentration decreases in places ultimately separated from the open water. The velocity of the succession is largely dependent on the size of the lake, but also on the degree of separation from the open water. Alongside the open water the effect of the decrease in quantity of essential minerals is only noticeable after a much longer time-span, whilst other factors such as the effect of the dash of the waves may also play an important rôle. The wash of the waves reduces the rate of succession, or may even cause erosion of the shores in larger lakes, for instance along the north-eastern side of the Beulakerwijde. At the leaside of larger lakes the vegetation develops not only more rapidly in the beginning, but also in a different fashion.

In the diagram the succession is indicated in the vertical direction, in a progressive sense from the top to the bottom. In the horizontal direction it proved to be impossible to consider a single factor as indicative of a gradient, because several (and, moreover, more or less correlated) factors are simultaneously operative in determining the differences in the developmental series of the vegetation. The most important is most probably the nutritional ecology, but this is in itself a very complex factor, the chemical factors requiring a separate analysis, but this must not obscure the mutual relations and interactions between these factors. The nutritional ecology is partly determined by the first factor to become the limiting one. From the chemical water analyses one might draw the conclusion that in this connection the phosphate content is the decisive one, but I do not subscribe wholeheartedly to this conclusion which is reported so often in the relevant literature (see under 5). The nutritional ecology is, in its turn, largely dependent on the methods of agricultural exploitation such as reed

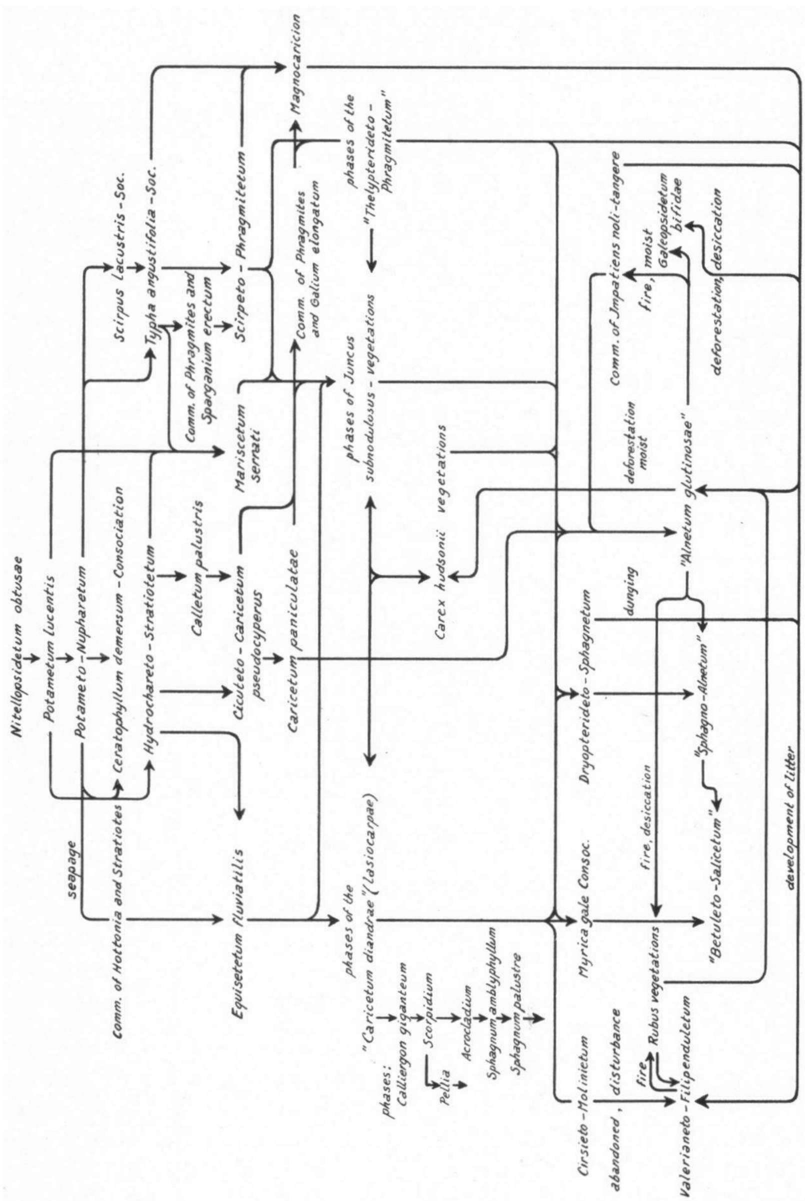

Fig. 2. Reduced scheme of the hydroseres in peat-bog vegetations in the north-western part of the province of Overijsel.

cutting and mowing, of irrigation, and of dunging (either directly, or indirectly by the effluent of hay fields treated with fertilisers running into the peat pits).

In the horizontal direction the following factors can be read according to a certain gradient: from left to right, an increasing total ion concentration in the substratum, an increasing effect of disruptive forces in the milieu, a decreasing influence of seepage phenomena. Disruptional forces are, among other things, the effect of dunging or of other pollutions of the environment. At the left side are situated those hydroseres which occur in peat holes which from the very beginning were never directly connected with open water, and at the right the hydroseres of open water appear. Hydroseres of the wind-sheltered margins of medium-sized lakes or of smaller ones in direct connection with open water, are found near the centre of the diagram.

One must imagine that in the horizontal direction all seres are linked by series of *transitional* stages. It is to be regretted that the diagram cannot be extended in more dimensions, which would provide a much clearer picture.

4.3. *Initial hydrosere vegetations*

When the peat digging reached the mineral subsoil (which is by no means always the case in places with substantial peat deposits), the initial vegetation in clear, unpolluted water consists of *Characeae.* This is also the case in open water with a sandy subsoil, as in the Zuideindigerwijde and the Bovenwijde. In this case the vegetation consists usually of (mainly) *Nitellopsis obtusa* and *Chara verrucosa,* which species may be characteristic of a *Nitellopsidetum obtusae,* described by DAMBSKA in 1961 (according to KRAUSCH, 1964). Almost invariably the initial vegetation consists of elodeids. In larger lakes larger elodeids occur, especially *Potamogeton lucens.* The *Potametum lucentis* can be succeeded by the *Potameto-Nupharetum* (described by MULLER & GÖRS, 1960; the vicariating *Myriophylleto-verticillati-Nupharetum* is characteristic of montane regions).

In places situated in the lea side of the smaller lakes, especially along the western margins (a good example is provided by the Zuideindigerwijde), and in closed peat holes the *Hydrochareto-Stratiotetum* develops, in eutrophic open waters usually via a phase in which *Ceratophyllum demersum* occurs abundantly. The development of the *Stratiotetum* is mainly dependent on the presence of a minimum deposit of sapropelium. That this deposit occurs chiefly in wind-sheltered places, is attributable to the activity of wind, causing not only a dash of waves at the water surface but also an undercurrent in the opposite direction. The undercurrent is probably responsible for the deposit of fine sediments, and of plant debris, in the wind-sheltered places. The initial phase of the *Hydrochareto-Stratiotetum* consists of a vegetation of *Stratiotes* plants which rest on the layer of soft sapropelium. It is only after the population has become so dense that the lower leaves, which stick out laterally in all directions, touch each other, when the plants start floating just below the surface. They apparently lift each other to the surface by the mutual pressure of the radiating lower leaves. In a zonation of the vegetation the development from submerged to emergent *Stratiotes* plants can often be observed very clearly. The *Hydrochareto-Stratiotetum* constitutes the terminal stage of the hydrophase of such hydroseres. It is a vegetation with an intricate structure, consisting of stratiotids, hydrocharids, ceratophyllids, and frequently also lemnids and ricciellids (DEN HARTOG & SEGAL, 1964; SEGAL, 1965). Apart from *Stratiotes aloides* and *Hydrocharis morsus-ranae*, *Utricularia vulgaris* also occurs in water which is not too heavily polluted. In open water a floating hydrosere phase can develop out of this *Hydrochareto-Stratiotetum*, in which floating masses of vegetation appear, in this case the *Cicuteto-Caricetum pseudocyperus*, which may be preceded by the *Calletum palustris*. This *Cicuteto-Caricetum pseudocyperus* consists of impassable floating vegetation islands in which frequently *Cardamine palustris* occurs. The *Caricetum paniculatae* is another vegetation of floating islands, but it occurs in places where the layer of sapropelium is considerably thicker.

The succession in places exposed to the wash of waves is usually altogether different. The development of a vegetation of pleustophytes, or of forms which are only lightly anchored in the soft sapropelium, is of course precluded. Nymphaeids, on the other hand, are relatively well adapted to a gentle wave dash, whilst in fairly shallow places *Scirpus lacustris* and in the shallower parts *Typha angustifolia* can establish themselves. These *Scirpus* and *Typha* vegetations are the forerunners of other helophyte vegetation types of the *Phragmitetea*, which is evident from the occurence of subsequent succession phases adjoining the *Scirpus* and *Typha* stages. It appears that the pioneer species in these seres have a wide "ecological amplitude". During the succession, gradually more species with a relative narrower ecological amplitude get a chance of establishing themselves. This rule does not hold only for hydroseres, but also applies to other succession types.

4.4. *Succession in seepage areas*

After the establishment of the initial hydrophyte vegetation in isolated peat holes frequently a community develops locally in very sheltered places alongside the *legakkers*, which contains *Hottonia palustris* and the submerse form of *Stratiotes aloides*, more particularly in spots where there is a considerable percolation of water. In small and in narrow peat holes as well as in sheltered places a vegetation of *Equisetum fluviatile* develops out of the *Hydrochareto-Stratiotetum*, the *Equisetetum fluviatilis*. On a thick but not very solid sapropelium deposit *Equisetum fluviatile* forms a net of rhizomes at a depth of about 0,5 m, on which subsequently such species as *Carex rostrata* and *Lysimachia thyrsiflora* get a foothold in the meshes, thus leading in the initial stage of the "*Caricetum diandrae*". Especially in places where the mineral subsoil within a seepage area is rather shallow, *e.g.*, in places where sand ridges occur, the succession may initially proceed by way of a *Cladium mariscus* vegetation which is poor in species, and which may exist for a long time.

Next to the *Caricetum diandrae* the (*Phragmiteto- and Eriophoreto-*) *Caricetum lasiocarpae* has been recognized (cf. KUIPER, 1958, PASSARGE, 1964), but this distinction cannot be maintained here, because *Carex lasiocarpa* and *Carex diandra* grow mixed in all numerical proportions, and even in the extreme cases of dominance of one of the two species no differential species can be recognised. There is, nevertheless, a slight difference in ecology, *C. lasiocarpa* often occurring more frequently, or as the dominant species, in the early phases of the hydrosere, and *C. diandra* being more typical of a seepage area than *C. lasiocarpa*. The latter species apparently prefers more eutrophic habitats, but at the same time tolerates greater fluctuations in the ion composition of the water. This assumption is in good agreement with the occurrence of *C. lasiocarpa* in the lagg zones of certain types of peat bogs. However, it is also an open question if the various phases can be considered to represent one association. The initial phases differ so much from the later ones that they usually have but few species in common, and if they have, the common species still exhibit an appreciable difference in abundance and in vitality. It will eventually prove to be necessary to split up the so-called *Caricetum diandrae* in at least four associations which may even have to be partly referred to different alliances, *viz.*, to the *Scorpidion* (cf. DU RIETZ, 1949), the *Sphagnion amblyphylli*, and the *Sphagnion palustris*. In each of these alliances a number of associations can be recognised (cf. the review in DUVIGNEAUD, 1949). When the succession series are well developed, the following stages are present:

1. The *Calliergon giganteum* phase. The water level almost constantly remaining higher than the soil surface, pH between 8.0 and 6.5. The differential species belong to the *Phragmition* and the *Stratiotion*, more particularly to the *Equisetetum fluviatilis* and the *Hydrochareto-Stratiotetum: Equisetum fluviatile*, *Carex rostrata*, *Lysimachia thyrsiflora*, and *Utricularia vulgaris*, and in addition, apart from *Calliergon giganteum*, also *Marchantia polymorpha* f. *aquatica*, *Riccia fluitans* ssp., *Chara globularis* and *C. aculeolata*. This phase is often only fragmentarily developed and in this case not so easily distinguishable from the preceding and subsequent phases.

2. The *Scorpidium* phase. This is usually, in combination with the subsequent phase, regarded as representing *the* optimum stage of the *Caricetum lasiocarpae* or *Caricetum diandrae*. The water level is, at least in the gullies, a few cm above the soil surface for most of the year. The pH fluctuates between 7,5 and 6.1, the optimum pH lying between 6.2 and 6.5. Strikingly large fluctuations in the pH values are highly characteristic of this phase; this is inherent in seepage phenomena. It is a mistake to ascribe the relative scarcity of species of *Scorpidium*, *Drepanocladus*, *Campylium*, etc. to a narrow ecological amplitude; up to

a point the opposite is true. Differential species are *Scorpidium scorpioides*, *Drepanocladus lycopodioides*, *D. intermedius*, *Campylium stellatum*, *C. polygamum*, *C. elodes*, *Riccardia pinguis*, *R. multifida*, *Utricularia intermedia*, *U. minor*, *Eriophorum gracile* and *Pedicularis palustris*.

Usually *Carex lasiocarpa* shows optimum development in this phase. One can distinguish a variant with *Thelypteris palustris* in more eutrophic habitats, and one with *Menyanthes trifoliata* in the more typical undisturbed seepage areas.

3. The *Pellia* phase. This phase appears, as a rule, as a locally raised vegetation type within the *Scorpidium* belt. The transistion to the next phase is rarely a sharp one, and a clear-cut zonation of this phase between the *Scorpidium* and *Acrocladium* zones is often lacking. This is partly because of the considerable competitive capacities of *Acrocladium cuspidatum*, which is capable of penetrating into the *Scorpidium* zone. This phase is, accordingly, much restricted in area and in time, especially where the zonation is already crowded. That pleurocarpic mosses not infrequently get the upper hand over acrocarpic mosses and liverworts, is in a large number of vegetation types the rule rather than the exception. The raised portions in the *Scorpidium* phase are normally flooded during the winter, but in the summer a slight superficial desiccation may occur. This may cause appreciable fluctuations in the pH values and ionic concentrations. The upper limit of the pH is somewhat lower than that of the *Scorpidium* phase, the pH varying between 7.2 and 5.9. Ecologically and systematically this vegetation type can best be classified in the *Scorpidion*. Differential species are *Pellia neesiana* (already present in the *Scorpidium* phase), *P. epiphylla*, *Bryum pseudotriquetrum*, *B. bimum*, *Mnium pseudopunctatum*, *M.* (*affine* ssp.) *rugicum*, *Fissidens adiantoides*, *Linum catharticum*, *Sagina nodosa*, *Liparis loeselii*, *Epilobium palustre* and *Cardamine pratensis*. Many of these species are higher plants of low stature with a shallow root system which is developed in the bryophyte layer. *Sagina nodosa* and *Linum catharticum* frequently attain their optimum in the subsequent zone, provided the herb layer is not too well developed and the vegetation retains an "open" character. Also *Dactylorchis praetermissa* (inclusive of its var. *junialis*) reaches its optimum here, although it maintains itself in the next phase. Occasionally these species exhibit a second optimum development if the *Acrocladium* phase obtains an unusually sparse vegetation cover as the result of acidification, *i.e.*, in the terminal stages of this phase.

4. The *Acrocladium phase*. This phase often covers large areas. *Acrocladium cuspidatum* (*Calliergonella cuspidata*) not only has a considerably competitive power, but also a wide ecological amplitude. The ground water level does not often lie above the surface of the soil. The pH varies between 6.8 and 4.9. The optimum average pH lies between 5.7 and 6.2. Differential species: *Acrocladium cuspidatum*, *Calamagrostis neglecta*, *Dactylorchis incarnata*, *Parnassia palustris*, *Valeriana dioica*, *Stellaria palustris* var. (ssp.?) *viridis* and *Agrostis canina* ssp. *stolonifera* (*A. stolonifera* var. *turfosa*).

Menyanthes trifoliata often shows its maximum development in this phase, but may also dominate already in the *Scorpidium* phase. The same holds for *Carex diandra*. This phase can persist for a considerable length of time. When the vegetation covers a large surface area, *Acrocladium* is frequently the only moss species and at any rate always the dominant one. Only in gullies and in the more elevated parts is this not always the case.

5. The *Sphagnum amblyphyllum* phase. This phase mostly starts with the formation of small elevated areas in the *Acrocladium* phase, but it can be very extensive and can persist for a long time. Occasionally the development of raised areas and gullies may be so pronounced that a pattern can be observed of *Acrocladium* or even *Scorpidium* vegetations in the gullies and *Sphagnum* vegetation on the raised portions. The water level remains below the surface for the most part of the year and as a rule lies 10 cm or more below the surface. The pH varies from 5.7 to 4.2, the optimum average pH lies between 4.7 and 5.0. Differential species: *Sphagnum amblyphyllum* (*S. recurvum* ssp. *amblyphyllum*), *S. fimbriatum. S. contortum, S. plumulosum, S. teres, S. squarrosum* (also in the next phase), *Calypogeia trichomanis, Potentilla erecta, Comarum palustre, Viola palustris, Carex curta, C. echinata, Hydrocotyle vulgaris* and *Salix repens*.

The role of *Menyanthes trifoliata* which frequently determined the aspect of the vegetation in the two preceding phases, declines. When the vegetation develops towards the next phase—which usually happens in those places where the solidification of the soil has been relatively slow as is the case between the balks—low shrubs, primarily *Salix repens*, and later on particularly *Myrica gale*, may dominate. Up against the balks, on more thoroughly compacted soil, and already in the *Acrocladium* phase, for that matter, a number of species of the *Cirsieto-Molinietum* may appear, such as *Carex pulicaris, C. panicea, C. hostiana, C. demissa, Succisa pratensis, Molinea coerulea, Viola canina*, and eventually even *Carex buxbaumii* and *Cirsium dissectum*. In this case the vegetation may gradually develop into the *Cirsieto-Molinietum caricetosum buxbaumii* (Segal & Westhoff, 1959). A related vegetation type may develop after the establishment of *Molinia* tussocks.

6. The *Sphagnum palustre* phase. Also this phase may initiate by the formation of elevated areas. Since the more typical species are even considerably more susceptible to fertilisers and other disturbing influences than the species predominating in the preceding phases, the *Sphagnum palustre* phase is nowadays only fragmentarily developed. Moreover, the succession often does not reach this phase, because the establishment of seedlings, especially of *Alnus glutinosa, Salix aurita* and *S. cinerea*, during a previous phase, may divert the succession in the direction of the alder marsh grove if the vegetation is not regularly mowed. In both *Sphagnum* phases, in addition to these other woody plants, *Betula pubescens* and sometimes *Sorbus aucuparia* may become established, so that in this case the succession may proceed in the direction of a *Betuleto-Salicetum* (*Franguleto-Salicetum auritae*). The water table lies upon the average at least 10 cm below the surface. The pH varies

from 5.5 to 4.0 with an optimum at 4.3-4.5. Differential species: *Sphagnum palustre*, *S. papillosum*, *S. rubellum* (rare), *S. subsecundum*, *S. recurvum* (ssp. *recurvum*), *Aulacomnium palustre*, *Polytrichum commune* var. *uliginosum*, *P. marginatum*, *Pohlia nutans* var. *sphagnicola*, *Calliergon stramineum*, *Cephalozia connivens*, *Eriophorum angustifolium*, *E. vaginatum* (very rare), *Drosera rotundifolia* and even *Erica tetralix* and *Oxycoccus palustris*, and the mushrooms *Galerina sphagnorum*, *G. paludosa*, *G. tybiicystus*, *Hygrophorus turundus* and *Mycena swartzii*.

In this stage there is, properly speaking, no question of a *Caricetum lasiocarpae*, or a *Caricetum diandrae* any longer. The vegetation has usually only a few species in common with the *Scorpidium* phase, and in its most extreme (acid) variants not even a single one.

True peat-moor vegetation does not develop in the area under discussion. In the Wanneperveen area the lowest pH value recorded was 3.7, measured in vegetation of *Erica* and *Oxycoccus* with a distinct fragmentary character (Bollemaat, near Kerkgracht). It is problematical whether a succession can culminate in an oligotrophic and ombrogenous peat-moor. Probably such a development is prevented, apart from disturbances caused by agricultural practice, by geographical factors such as water percolation. At any rate, no vegetation types were encountered which are comparable with the typical oligotrophic *Sphagnum* communities of the diluvial regions. The succession can hardly anywhere be clearly traced step by step, but in a number of places a development into a *Betuleto-Salicetum* can be observed, with most frequently a *Myrica* consociation as the intermediate phase. (I do not know if this interphase corresponds with the *Myricetum gale* as it was originally described, and which is referred to the *Ombrosphagnetea*). The association found in the area under discussion belongs to the *Sphagnion palustris*, the classical *Caricion canescentis-fuscae* (NORDHAGEN, 1936) or the (in the first place physiognomically characterised) *Salicion auritae* (DOING, 1962).

It will be understood that in this survey the succession is only sketched in broad outlines. Often greater or smaller deviations occur locally. Sometimes it may be advisable to describe the succession in more detail. On a site near the Hogeweg at Oldemarkt it is possible to ascertain (by means of a study of the microdistribution of the species within the vegetation), with a fair degree of accuracy, the sequence of appearance of the following species which are numerically dominant in smaller or larger areas: *Chara*-species with *Utricularia vulgaris*, *U. minor* with *Scorpidium*, *U. intermedia* with *Scorpidium*, *Calliergon giganteum*, *Campylium elodes*, *C. stellatum*, *Drepanocladus lycopodioides*, *Bryum pseudotriquetrum*, etc.

Especially in the more disturbed situations the succession proceeds via the *Dryopterideto-Sphagnetum*, in which *Dryopteris cristata*, *D. carthusiana* (=*D. spinulosa*) and the rare *Osmunda regalis*, sometimes also *Lonicera periclymenum* constitute the more characteristic species. However, this association is also found, more particularly outside N.W. Overijsel and the Vechtplassen area, in *S. recurvum* communities, where it achieves its optimum development. The *Dryopterideto-Sphagnetum* is a wide-spread plant community of more or less disturbed hydroseres and has not only been found in the Netherlands in many places, but also in Britain, Belgium, Germany, Poland and Sweden.

If the peat-bog vegetations are not maintained by mowing (for hay making), there develops either fenn carr (after the establishment of tree seedlings), or a vegetation cover of tall herbs, the *Valerianeto-Filipenduletum,* particularly when a layer of vegetable litter of some depth has accumulated, and if a previous phase contained species of the *Cirsieto-Molinietum.* This type of vegetation may also develop following some forms of disturbance such as burning, dunging, or the application of fertilisers and herbicides. An important interference in the natural succession series in most cases results in a dominance of *Calamagrostis canescens.*

4.5. *The succession in open water*

The succession described in the preceding paragraphs proceeds at an optimum rate in hydroseres of isolated or secondarily closed-in peat pits in a seepage zone. In open water most frequently parallel series are encountered, whose floristic composition is mainly dependent on the relative abundance of nutrients, percolation (vertical water movements), and various anthropogenic influences. In an environment rich in nutrients the *Caricetum diandrae* is replaced by the *Thelypterideto-Phragmitetum.* The initial phase is often accompanied by a lemnid community of *Lemna minor* and *Ricciocarpus natans,* the *Ricciocarpeto-Lemnetum* (SEGAL, 1963). *Calliergon giganteum* is quite often present in small quantities in the next phase, but the *Scorpidium* phase is often completely lacking, and in the *Pellia* phase, among other species, *Drepanocladus aduncus, Pallavicinia lyellii* and *Chiloscyphus polyanthus* are the differential species. Where the *Thelypterideto-Phragmitetum* develops from "floating island" communities, the initial phase mostly consists of a reed vegetation which contains *Galium palustre* ssp. *elongatum, Solanum dulcamara* and *Sium erectum,* the so-called *Scirpeto-Phragmitetum solanetosum.* The *Pellia* phase is normally present and well-developed, but poorer in species than in *Carex lasiocarpa* vegetation. *Pellia epiphylla, Marchantia polymorpha* f. *aquatica* and *Mnium affine* are the most important species, frequently accompanied by *Plagiothecium ruthei, Brachythecium rutabulum* and *Lophocolea heterophylla.* The floristic composition of the subsequent phases tends to become parallel with that of the *Caricetum diandrae* phases, but it does not culminate in a *Cirsieto-Molinietum.* Generally speaking the phases are poorer in species and thus negatively characterised in respect of the *Caricetum diandrae* series. On the other hand some species are clearly better developed in the *Phragmitetum* series, especially *Thelypteris palustris* and *Comarum palustre,* which partly replace *Menyanthes trifoliata.* In addition, *Eupatorium cannabinum* and *Lycopus europaeus* are present, and in the later phases *Dryopteris cristata, D. carthusiana* and *Hydrocotyle* *vulgaris*. The *Thelypterideto-Phragmitetum* yields reed of outstanding quality, at least in its younger stages. Provided the reed is not cut at regular intervals, the accumulation of a layer of litter proceeds more readily than in the vegetation types of the"floating tussocks", so that intermediate types develop leading to the *Valerianeto-Filipenduletum*. Such vegetations may cover large areas. As a rule they develop out of the *Sphagnum amblyphyllum* phase in which the reed stand has degenerated to such an extent that cutting is no longer considered worth while. The degeneration of the reed is thus accelerated. The reed exploitation can be saved in such cases by the artificial regulation of the water table by drains. The *Sphagnum amblyphyllum* phase usually proceeds towards the *Dryopterideto-Sphagnetum*.

4.6. *Other hydroseres*

An intermediate position is occupied between the "*Caricetum lasiocarpae*" and the *Thelypterideto-Phragmitetum* by the series of *Juncus subnodulosus* vegetations. The use of the name "*Menyantheto-Juncetum subnodulosi*" is better avoided, because the *Juncus subnodulosus* communities lack differential species and must be considered to represent (mostly) impoverished forms of *Carex lasiocarpa* vegetation, in which *Juncus subnodulosus* is aspect-forming and takes the part of *Carex lasiocarpa* or *C. diandra*. For similar reasons such names as *Phragmiteto-Caricetum lasiocarpae* or *Eriophoreto-Caricetum lasiocarpae* must be discarded. The name *Thelypterideto-Phragmitetum*, on the contrary, could be maintained, but, properly speaking, one should include only the earlier stages, up to and including the *Pellia* phase. The *Juncus subnodulosus* series may in most cases be considered to be a more or less disturbed sere of the so-called *Caricetum lasiocarpae*. The disturbance is mostly caused by increasing eutrophy, either through drainage control, or after pollution by fertilisers. This is apparently the reason why *Juncus subnodulosus* communities often appear in narrow strips alongside balks treated with fertilisers. I think it is not very probable that this phenomenon must be ascribed to the more solid substratum, as KUIPER (1958) surmised. An argument in favour of my explanation is the fact that in the *Juncus* series usually more indicators of disturbance zones occur. *Juncus* species themselves are generally such indicators of zones of interference. According to Kuiper *Menyanthes* is reputed to be more "opulent" in the *Juncus* series than in the *Caricetum diandrae* series, but this is upon the whole not true and rather the reverse is the case. *Juncus subnodulosus* vegetation can also develop from the initial phases of the *Thelypterideto-Phragmitetum* communities, but only if the isolation from the open water is completed at an early stage of the succession. The *Juncus subnodulosus* vegetations thus appear to be somewhat intermediate, in an ecological sense, between the two other seres. This also holds true for its floristic composition.

A fourth parallel series consists of *Carex hudsonii* vegetations. They usually develop on felled alder carrs and not infrequently they form a zone between such groves and the more typical peat-moor vegetation. *Calliergon* and *Scorpidium* phases are lacking. The uneven vegetation cover of the soggy peat fens usually forms transitions to the *Juncus subnodulosus* or *Carex lasiocarpa* series. There is here no question of a "*Caricetum elatae*". The community has neither floristically nor physiognomically anything to do with a *Magnocaricion* vegetation.

It is noteworthy that the pH ranges in the parallel seres are somewhat different from the range recorded from the *Caricetum diandrae.* Generally speaking the pH ranges are somewhat shifted towards higher pH levels, at least in the earlier phases. In the *Scorpidium* phase of the *Thelypterideto-Phragmitetum,* for instance, the range lies between 8.0 and 6.2. The seemingly unimportant differences could perhaps, at least partly, explain the differences in the combinations of species, but presumably certain nutrients and differences in the water relations (e.g. the water table and a changing water level) may contribute, apart from the differences in initiation, which partly depend on the structural features of the landscape.

In the diagram is indicated, from left to right, an increase in nutrients or of disturbing effects leading to an increased pollution. It is roughly possible to outline a range of the following, often dominant species: *Carex diandra, C. lasiocarpa, Juncus subnodulosus, Phragmites communis, Carex acutiformis, Glyceria maxima.* In this series the differentiation in many successional stages is manifest in the first two species, but diminishes gradually. In the *Phragmites* stands mostly only two or three phases can be clearly distinguished, but in the *Magnocaricion* stands only rarely two phases develop.

4.7. *Examples*

As illustrative examples, two tables are shown (borrowed from SEGAL, 1963) of zonations in the Wanneperveen area, in places where, incidentally, the vegetation does not show optimal development. Table 1 gives an impression of the hydrosere of an isolated peat pit. Vegetation record 1 shows a normal *Potameto-Nupharetum,* record 2 a *Hydrochareto-Stratiotetum* with a first appearance of helophytes, record 3 an *Equisetetum fluviatilis* with, as is the rule, occasional species persisting from the preceding zones. This example was slightly disturbed, presumably by the application of fertilisers in the neighbourhood, as can be deduced from the occurrence of certain *Lemna* species and of *Carex acutiformis.* Record 4 is representative of a fairly far advanced stage of the *Scorpidium* phase, record 5 of an early stage of the *Acrocladium* phase, and record 6 of a typical *Sphagnum amblyphyllum* phase. Record 7 has, up to a point, an ambivalent character, on the one hand *Myrica* being abundant and on the other hand the proportion of *Molinion* species being rather high. The experimental area was not quite homogeneous, but it did not prove to be possible to find homo-

TABLE 1

Hydrosere of an isolated peat pit in De Landen achter 't Singel between Belt–Schutsloot and Zwartsluis.

Number of record			1	2	3	4	5	6	7
Year			1960	1960	1960	1960	1960	1960	1961
Date			4VIII	18VII	4VIII	4VIII	4VIII	4VIII	15IX
Surface (m^2)			100	100	25	10	10	10	10
Percentage water-surface			100	100	100	50	5	0	0
Ground water level (m)			+1,6	+0,9	+0,3	+0,05/0	0	—0,15	—0,15
Specific conductivity ($\varkappa_{18} \times 10^6$)			342	–	–	82	67	68	–
pH-H_2O			6,9	–	–	6,3	5,7	4,7	–
Cl^-	(mg/l)		50,1	–	–	10,4	11,2	16,5	–
HCO_3^-	(mg/l)		157	–	–	33	16	16	–
NH_4^+	(mg/l)		0,40	–	–	0,11	0,17	0,36	–
Organic ammonium	(mg/l)		0,64	–	–	2,2	2,4	4,0	–
Total hardness	(°D)		8,5	–	–	1,8	1,5	1,3	–
Bicarbonate hardness	(°D)		7,2	–	–	1,5	0,7	0,7	–
Ca^{++}	(mg/l)		49,8	–	–	10,8	7,8	5,5	–
PO_4^{---}	(mg/l)		0,1	–	–	0,1	0,7	3,0	–
SO_4^{--}	(mg/l)		4,3	–	–	7,0	11,5	6,6	–
Nymphaeids	covering')	(%)	40	s	3	s	–	–	–
Hydrocharids	,,	(%)	s	20	20	s	–	–	–
Ceratophyllids	,,	(%)	s	3	s	25	–	–	–
Stratiotids	,,	(%)	–	80	–	–	–	–	–
Hottoniids	,,	(%)	–	3	2	–	–	–	–
Elodeids	,,	(%)	–	1	1	–	–	–	–
Lemnids	,,	(%)	–	–	s	–	–	–	–
Ricciellids	,,	(%)	–	–	s	–	–	–	–
Layer of Bryophytes	,,	(%)	–	–	–	70	80	100	90
,, ,, herbs	,,	(%)	–	3	25	35	60	40	40
,, ,, ,,	height	(m)	–	0,1/0,8	0,1/0,8	0,2/0,8 (1,2)	0,2/0,8 (1,2)	0,4/(1,2)	0,4(1,2/ 2,5)
Total number of species			5	11	29	42	45	35	53

s means: sparse (< 1 %).

		1	2	3	4	5	6	7
Species of the Nymphaeion								
Ch. All.	Nymphaea alba	2b.2	+r.1	1b.2	+p.2°	–	–	–
Ch. Cl.	Potamogeton natans	+r.1	+r.1	+r.1	–	–	–	–
Ch. All.	Nuphar luteum	2b.2	–	–	–	–	–	–
Ch. Cl.	Elodea canadensis	–	1a.1	–	–	–	–	–
Ch. Cl.	Fontinalis antipyretica	–	–	1p.2	–	–	–	–
Species of the Stratiotion								
Ch. Cl.	Ceratophyllum demersum	+p.2	–	–	–	–	–	–
Ch. Ord.	Hydrocharis morsus-ranae	r.2	2b.2	2b.2	+p.1°	–	–	–
Ch. Ass.	Utricularia vulgaris	–	1b.1	+p.1	–	–	–	–
D. Comm.	Hottonia palustris	–	1b.1	1b.1	–	–	–	–
Ch. All.	Stratiotes aloides	–	5a.5	–	–	–	–	–
D. Comm.	Myriophyllum verticillatum	–	–	+p.1	–	–	–	–
Ch. Cl.	Lemna minor	–	–	+p.2	–	–	–	–
D. Cl.	Lemna trisulca	–	–	+p.2	–	–	–	–
Species of the Phragmition								
Ch. Ord.	Phragmites communis	–	1b.2	1p.1	+p.1	+p.1	–	+p.1–2
D. Comm.	Equisetum fluviatile	–	1p.1	2m.5	2m.1	2m.1	+p.1	+p.1
Ch. All.	Ranunculus lingua	–	+p.1	1a.1	+r.1	–	–	–
Ch. Ord.	Typha angustifolia	–	1p.1	+r.1	–	–	–	–
D. Comm.	Lysimachia thyrsiflora	–	–	1p.1	+r.1	+p.1	–	–
D. Comm.	Carex rostrata	–	–	+p.1	+r.1	–	–	–
Cicut.	Cicuta virosa	–	–	1a.1	–	–	–	–
Cicut.	Carex pseudocyperus	–	–	1p.1	–	–	–	–
Ch. Cl.	Alisma plantago-aquatica	–	–	1p.1	–	–	–	–
Ch. All.	Acorus calamus	–	–	+p.1	–	–	–	–
Ch. Cl.	Galium palustre	–	–	+r.1	–	–	–	+p.1
Magnoc.	Carex acutiformis, veg.	–	–	+p.1	–	–	–	–
Magnoc.	Carex hudsonii, veg.	–	–	–	–	–	–	+p.2

TABLE 1 (*continued*)

Species of the Caricion lasiocarpae		1	2	3	4	5	6	7
+ Phragm.	Mentha aquatica	–	–	+r.1	+p.1–2	+p.1	+p.1	+p.2
D. All.	Menyanthes trifoliata	–	–	+r.1	+p.2	+a.1	+r.1	–
Ch. All.	Carex lasiocarpa	–	–	–	2b.2	2m.2	2m.2	2m.5
Ch. Ord.	Pedicularis palustris	–	–	–	2a.1	+p.1	+r.1	–
D. Ord.	Juncus subnodulosus	–	–	–	1a.2	+p.1	+p.1	+p.1
Ch. All.	Eriophorum gracile	–	–	–	1p.1	+p.1	–	–
D. Scorp.	Campylium stellatum	–	–	–	2a.4	2m.2	–	–
D. Scorp.	Scorpidium scorpioides	–	–	–	4a.5	–	–	–
D. Scorp.	Utricularia intermedia	–	–	–	2b.2	–	–	–
D. Scorp.	Utricularia minor	–	–	–	2a.2	–	–	–
D. Scorp.	Chara aculeolata	–	–	–	1b.2	–	–	–
D. Scorp.	Drepanocladus lycopodioides	–	–	–	1p.2	–	–	–
D. Scorp.	Drepanocladus fluitans	–	–	–	+p.2	–	–	–
D. Scorp.	Campylium polygamum	–	–	–	+p.2	–	–	+r.1
D. Scorp.	Riccardia multifida	–	–	–	+p.2	–	–	–
D. Scorp.	Pellia neesiana	–	–	–	+p.2	–	–	–
D. Scorp.	Epilobium parviflorum	–	–	–	+r.1	–	–	–
+ Mol.	Peucedanum palustre	–	–	–	+p.1	+p.1	+p.1	–
+ Mol	Dactylorchis praetermissa	–	–	–	1a.1	+p.1	–	–
+ Mol.	Dactylorchis praet. var. junialis	–	–	–	+p.1	+p.1	–	–
Ch. Ord.	Liparis loeselii	–	–	–	1p.1–2	1a.1	–	–
+ Mol.	Valeriana dioica	–	–	–	+p.1	2a.1	2a.1	+r.1
Ch. All.	Carex diandra	–	–	–	2a.2	2b.2	2a.2	+p.2
Ch. Ord.	Parnassia palustris	–	–	–	1p.1–2	2a.2	+p.1	+p.1
Ch. All.	Calamagrostis neglecta	–	–	–	+p.1	+p.1	–	+r.1
Ch. Ord.	Bryum pseudotriquetrum	–	–	–	1p.3	2m.2	+p.2	–
Ch. Ord.	Dactylorchis incarnata	–	–	–	1a.1	1b.1	–	–
D. Ord.	Pellia epiphylla	–	–	–	1p.2	2a.3	–	–
D. Acrocl.	Acrocladium cuspidatum	–	–	–	–	4a.4	1p.2	+r.2
D. All.	Agrostis canina	–	–	–	–	2a.2	1p.2	1p.2
D. All.	Fissidens adiantoides	–	–	–	–	1p.2	+r.2	–
Ch. All.	Mnium pseudopunctatum	–	–	–	–	2m.2	–	–
D. Ord.	Sagina nodosa	–	–	–	–	1p.2	–	–
D. Ord.	Linum catharticum	–	–	–	–	1p.1	–	–
Ch. Ord.	Mnium rugicum	–	–	–	–	+p.2	–	–
Ch. All.	Stellaria palustris var. virescens	–	–	–	–	+r.1	–	–

Species of the Caricion canescentis-fuscae		1	2	3	4	5	6	7
D. All.	Hydrocotyle vulgaris	–	–	–	–	+p.1	+p.1	+p.1
D. All.	Salix repens	–	–	–	–	+p.1	+p.1	+p.1
D. All.	Betula pubescens	–	–	–	–	+p.1	+p.1	1p.3
D. All.	Potentilla erecta	–	–	–	–	1a.2	1b.2	–
Ch. All.	Calypogeia trichomanis	–	–	–	–	–	4b.5	3b.4
Ch. All.	Sphagnum amblyphyllum	–	–	–	–	–	4b.5	3b.4
D. All.	Sphagnum fimbriatum	–	–	–	–	–	2a.3	+p.2
Ch. All.	Comarum palustre	–	–	–	–	–	+p.1	+p.1
Ch. All.	Viola palustris	–	–	–	–	–	+p.1	+p.1
Ch. All.	Sphagnum teres	–	–	–	–	–	2a.2	–
Ch. All.	Sphagnum plumulosum	–	–	–	–	–	1a.2	–
D. All.	Aulacomnium palustre	–	–	–	–	–	2a.2–3	2m.2
D. All.	Myrica gale	–	–	–	–	–	1a.2	2b.3
D. All.	Sphagnum squarrosum	–	–	–	–	–	1a.2	2b.4
D. All.	Drosera rotundifolia	–	–	–	–	–	+p.1	1p.1
D. All.	Calliergon stramineum	–	–	–	–	–	+r.1	+p.1
D. All.	Cephalozia connivens	–	–	–	–	–	+r.2	+r.2
D. All.	Galerina sphagnorum	–	–	–	–	–	+p.1	+r.1
D. All.	Sphagnum palustre	–	–	–	–	–	–	2b.3
D. All.	Sphagnum papillosum	–	–	–	–	–	–	2m.3
D. All.	Sphagnum rubellum	–	–	–	–	–	–	1b.3
D. All.	Polytrichum commune var. uliginosum	–	–	–	–	–	–	+p.2
D. All.	Sieglingia decumbens	–	–	–	–	–	–	+p.2
Ch. All.	Hierochloë odorata	–	–	–	–	–	–	+p.2
D. All.	Luzula multiflora	–	–	–	–	–	–	+p.2
Ch. All.	Carex nigra	–	–	–	–	–	–	+r.2
D. All.	Eriophorum angustifolium	–	–	–	–	–	–	+r.1
Ch. All.	Carex curta	–	–	–	–	–	–	+r.2

TABLE 1 (*continued*)

		1	2	3	4	5	6	7
Species of the Molinion								
Ch. Cl.	Lythrum salicaria	–	–	1p.1	+p.1	–	–	+p.1
Ch. Ord.	Eupatorium cannabinum	–	–	+p.1	+r.1	+p.1	–	–
Ch. Cl.	Hypericum tetrapterum	–	–	+p.1	–	+r.1	–	–
Calth.	Caltha palustris	–	–	–	1a.1	+a.1	–	–
Calth.	Cardamine pratensis	–	–	–	+p.1	+p.1	–	–
Calth.	Lotus uliginosus	–	–	–	+r.1	–	–	–
Ch. Cl.	Calamagrostis canescens, veg.	–	–	–	–	+r.2	–	+p.1
Ch. Ord.	Sanguisorba officinalis	–	–	–	–	+r.1	+p.1	–
Ch. Cl.	Cirsium palustre	–	–	–	–	+p.1	–	–
Ch. Ord.	Valeriana officinalis	–	–	–	–	+r.1	–	–
Ch. All.	Carex panicea	–	–	+p.2	+r.3	–	+r.2	1b.1–2
Ch. All.	Succisa pratensis	–	–	–	–	+p.1	+p.1	1a.1
Ch. Cl.	Molinia coerulea	–	–	–	–	–	–	1b.3
Ch. Cl.	Galium uliginosum	–	–	–	–	–	–	1b.2
Ch. Cl.	Anthoxanthum odoratum	–	–	–	–	–	–	1p.1–2
Ch. Cl.	Lychnis flos-cuculi	–	–	–	–	–	–	+p.1
Ch. Ord.	Rhinanthus glaber	–	–	–	–	–	–	+p.1
Ch. Ord.	Euphrasia nemorosa ssp.	–	–	–	–	–	–	+p.1
Ch. Cl.	Holcus lanatus	–	–	–	–	–	–	+r.2
D. Ord.	Leontodon nudicaulis	–	–	–	–	–	–	+r.1
Ch. Ord.	Lysimachia vulgaris	–	–	–	–	–	–	+r.1
D. All.	Platanthera bifolia	–	–	–	–	–	–	(+r.1)
Species of the Alnion								
Ch. Cl.	Alnus glutinosa, juv.	–	–	+p.1	+r.1	+a.1	–	+p.1
Ch. Cl.	Salix aurita, juv.	–	–	+r.1	–	1a.1	–	+p.2

geneous portions of the respective phases which were large enough for an adequate recording of their vegetation. Such "mixed" vegetations are rather the rule than the exception for that matter. One cannot predict with a reasonable degree of certainty whether a *Molinion* or a *Sphagnum-Erica* vegetation will develop, or if perhaps a *Myrica* vegetation will get the upper hand. Nearly everywhere in N.W. Overijsel the succession never does culminate in such a phase, because the lands can, at this stage, easily be made into fairly good hay fields by the application of fertilisers.

In Table 2 a succession is shown in a *Thelypterideto-Phragmitetum* series by means of recordings made in two transects. Vegetation records 1 up to and including 5 were obtained in the SE corner of the Schutslotigerwijde, the recordings 6 up to 11 inclusive along a transect in the NE of this area, and 12 in its immediate vicinity. Record 1 shows a *Potametum lucentis*, 2 a *Potameto-Nupharetum*, 3 an initial *Scirpus lacustris* vegetation developing in the *Potameto-Nupharetum*, 4 a *Scirpus* sociation developed in open water, and 5 an initial stage of the *Scirpeto-Phragmitetum*. The succession in this series is principally a function of the thickness of the sapropelium layer; the nutrient content remaining practically the same. This is no longer the case in the subsequent phase of the series in which the pH falls of gradually. Record 6 is of a variant of the *Scirpeto-Phragmitetum*, which is more or less typical of such hydroseres, and for which e.g., *Lysimachia thyrsiflora* and *Utricularia minor* can be differential species. The floating vegetation layer consists of the *Ricciocarpeto-Lemnetum*. Record 7 shows an early *Scorpidium* phase. *Campylium polygamum* in this series usually replaces *Campylium stellatum* of the "*Caricetum diandrae*". Record 8 shows the *Pellia* phase, which is as a rule much better developed in this series than it is in the "*Caricetum diandrae*" and sometimes covers large areas. Differential species in respect of the *Caricetum diandrae* are *Pallavicinia lyellii*, *Chiloscyphus polyanthus*, *Plagiothecium ruthei*,, and probably also *Marchantia polymorpha* f. *aquatica*. Record 9 illustrates the *Acrocladium* phase. The bryophyte layer is in this layer usually richer in species than in the corresponding phase of the *Caricetum diandrae*. The differential species are *Brachythecium rutabulum*, *Calliergon cordifolium* and *Lophocolea bidentata*, which, like the differential species of the preceding series, are rather trivial forms with a fairly wide ecological range. Record 10 shows the early *Sphagnum amblyphyllum* phase. This phase may be developed as a separate zonation in the first zone, of which *Sphagnum squarrosum* is the dominant species, which zone is succeeded by another one with dominance of *Sphagnum fimbriatum*, which in turn can be replaced by a zone of *Sphagnum amblyphyllum*. A transition from this *Sphagnum amblyphyllum* phase to the *Sphagnum palustre* phase is seen in record 11, showing a *Dryopterideto-Sphagnetum*. Record 12, a "*Sphagneto-Alnetum*", does not really follow in the succession, the grove having originated in an earlier phase which corresponds more with the phase shown in record 10. Both the *Dryopterideto-Sphagnetum* and the *Sphagneto-Alnetum* may develop either in the earlier or in the later *Sphagnum* phases. *Rubus* cf *tereticaulis*, a species previously overlooked as an indigenous element of our flora, was recorded by Professor Dr. A. G. de Wilde in several localities in N.W. Overijsel. It belongs to a section which does not include any other indigenous species. It remains to be seen if our specimens are indubitably referable to *R. tereticaulis* ore represent an undescribed species. The *Dryopterideto-Sphagnetum* usually has more the character of a typical "*Caricion canescentis-fuscae*" vegetation, and if this is the case, such species as *Carex curta* and *C. echinata* are also present. Sometimes *Dryopteris cristata* and *D. carthusiana* already appear as young sporophytes in the *Pellia* phase, in which the prothallia develop and in which the sporophytes occasionally attain a locally high dominance.

Table 2 is somewhat differently arranged in comparison to Table 1. The groups of species are here primarily intended as representing groups of differential species of which the characteristic species are the special cases. An indication such as "*Scorpidion*", accordingly, intends to convey: "differential species of the *Scorpidion* alliance" as in the case of *Chiloscyphus polyanthus*, or even "characteristic species" as in the case of *Scorpidium*. The species occurring in the *Pellia* phase have been included in the *Scorpidion* in the same way as in the series of the "*Caricetum diandrae*".

In the table the use of the name *Filipendulo-Petasition* is avoided. This alliance does not form a natural entity, and has to be divided in a *Filipendulion* in a restricted sense and another one (*Petasition*?).

5. Some ecological notes

It is impossible, within this compass, to discuss all results of the ecological investigations. For reliable conclusions the number or recorded data is too low anyhow, the more so because the number of vegetation types and intermediate communities is so large. Only in a few cases, particularly in communities of aquatic plants, do the recorded data permit a fuller analysis.

The observations give some idea of the ecological environment of each vegetation type and of the individual species occurring in that vegetation. It is possible to put all those vegetation records together in which a particular species was found, and subsequently to estimate the minimum and maximum values of each factor measured in these recorded vegetation fragments and the average value of these factors. One thus obtains the ecological amplitude of every species within the boundaries of the area under investigation, which can be combined with the estimation of frequency curves of each taxon and of each estimated factor, provided the collected data permit such an evaluation. It is, in principle, possible to include relative abundance also in these calculations, and for this and for similar data processing we intend to use a computer in the near future. The autecology is thus approached by way of the synecology. This method of approach has an appreciable advantage over experimental autecological analyses in that one only uses data obtained from natural conditions and one can analyse

Table 2 *(continued)*

		1	2	3	4	5	6	7	8	9	10	11	12
Species of the Potametea													
Ord. Magnopot.	Potamogeton lucens	2a.2	+p.1	–	–	–	–	–	–	–	–	–	–
Ord. ,,	,, perfoliatus	+p.1	–	–	–	–	–	–	–	–	–	–	–
Cl.	Myriophyllum spicatum	+p.1	2b.2	1b.2	+p.2	–	–	–	–	–	–	–	–
Cl.	Elodea canadensis	+p.2	1a.2	+p.1	+p.1	–	–	–	–	–	–	–	–
All. Nymphaeion	Nymphaea alba	–	2b.2	2b.2	1b.2	–	–	–	–	–	–	–	–
All. ,,	Nuphar luteum	–	2a.2	2a.2	1b.2	–	–	–	–	–	–	–	–
All. ,,	Potamogeton natans	–	1a.2	1p.2	1b.2	–	–	–	–	–	–	–	–
Species of the Lemnetea													
Cl.	Ceratophyllum demersum	–	1p.2	+p.2	–	–	–	–	–	–	–	–	–
Cl.	Lemna minor	–	–	–	–	–	2a.2	2m.2	+r.1	–	–	–	–
Ass.	Ricciocarpus natans	–	–	–	–	–	2m.2	1p.2	–	–	–	–	–
Species of the Phragmitetea													
All. Phragmition	Scirpus lacustris	–	–	+p.2	2m.2	2m.2	+p.1	+r.1	–	–	–	–	–
Cl.	Phragmites communis					+r.1	2m.5	2a.2	2a.5	2a.5	2a.5	1p.1	+p.1°
All. Phragmition	Typha angustifolia					1a.2	1b.2	1p.2	+p.1	+r.1	+r.1°	–	–
Cl.	Mentha aquatica					–	1a.1	+p.1	1a.1	1a.2	+p.1	–	–
Scorpidion	Lysimachia thyrsiflora					–	1p.1	+p.1	+r.1	+r.1	+r.1	–	–
Cl.	Rumex hydrolapathum					–	–	+r.1	+r.1°	–	+r.1°	–	–
Cl.	Galium palustre					–	–	+r.1	+p.1	+p.1	–	–	–
All. Cicution	Cicuta virosa					–	–	1a.1	–	–	–	–	–
Cl.	Carex rostrata					–	–	+p.1	–	–	–	–	–
Species of the Parvocaricetea													
All. Scorpidion	Utricularia minor					–	1–2–2–	1p.2	–	–	–	–	–
Cl.	Comarum palustre					–	–	+p.1	1a.1	+p.1	+r.1	+r.1	1b.1
+ Alnetea	Thelypteris palustris					–	–	+p.1	2b.1	3b.1	2a.1	+r.1	–
+ Molinietea	Eupatorium cannabinum					–	–	+r.1	1a.1	+p.1	–	–	–
All. Scorpidion	Chara globularis					–	–	2b.2	2a.3	+p.2	–	–	–
All. ,,	Calliergon giganteum					–	–	+p.2	+p.2	+r.2	–	–	–
All. ,,	Riccardia pinguis					–	–	+p.2	+p.2	–	–	–	–
All. ,,	Scorpidium scorpioides					–	–	2a.4	–	–	–	–	–
All. ,,	Campylium polygamum					–	–	2m.3	–	–	–	–	–
Ord.	Juncus subnodulosus					–	–	+p.1	–	–	–	–	–

TABLE 2
Hydrosere of the SE corner of the Schutslotiger wijde.

Number of record	1	2	3	4	5	6	7	8	9	10	11	12
Date 1961	3VIII	3VIII	3VIII	3VIII	3VIII	4VIII	4VIII	4VIII	4VIII	4VIII	4VIII	4VIII
Surface (m^2)	100	50	50	50	50	25	25	25	25	25	25	50
Percentage watersurface	100	100	100	100	100	97	85	15	3	0	0	0
Ground water level (m)	+1,9	+1,8	+1,6	+1,5	+0,7	+0,2	+0,05	0	—0,04	—0,15	—0,3	?
pH (Lyphan)	7,9	7,9	7,9	7,9	7,8	6,9	6,7	6,5	5,1	5,7	5,0	4,5
Elodeids covering (%)	10	15	5	1	–	–	–	–	–	–	–	–
Nymphaeids ,, (%)	–	25	25	10	–	–	–	–	–	–	–	–
Ceratophyllids ,, (%)	–	1	1	–	–	5	20	10	–	–	–	–
Lemnids ,, (%)	–	–	–	–	–	8	2	ger.	–	–	–	–
Layer of Bryophytes ,, (%)	–	–	–	–	–	–	10	45	75	97	100	90
,, ,, small herbs, ,, (%)	–	–	–	–	–	2	3	20	50	10	5	3
,, ,, ,, ,, , height (m)	–	–	–	–	–	0,2/0,4	0,2/0,5	0,2/0,8	0,2/0,8	0,2/0,8	to 0,5	to 0,4
,, ,, tall herbs, covering (%)	–	–	s	3	5	7	10	10	8	5	1	s
,, ,, ,, ,, , height (m)	–	–	0,5	1,2	1,9	1,0/2,0	1,3/1,8	1,6/(2,8)	1,6/(2,0)	1,2/(1,7)	0,8	0,8
,, ,, shrubs, covering (%)	–	–	–	–	–	–	–	–	–	1	1	35
,, ,, shrubs, height (m)	–	–	–	–	–	–	–	–	–	0,7	0,7	0,5/2,5
,, ,, trees, covering (%)	–	–	–	–	–	–	–	–	–	–	–	40
,, ,, ,, , height (m)	–	–	–	–	–	–	–	–	–	–	–	(2,0)/8,0
Total number of species	4	7	7	6	3	8	21	34	42	34	29	24

TABLE 2 (*continued*)

		1	2	3	4	5	6	7	8	9	10	11	12
All. Scorpidion	Chiloscyphus polyanthus							+p.2	2a.2	2a.2–3	+p.2	–	–
All. ,,	Pallavicinia lyellii							–	3b.2	2m.2	+p.2	–	–
All. ,,	Pellia epiphylla							–	2m.2	1p.2	+p.2	–	–
All. ,,	,, neesiana							–	1p.2	+p.2	–	–	–
All. ,,	Marchantia polymorpha f. aquatica							–	1p.2	+p.2	–	–	–
All. ,,	Bryum pseudotriquetrum							–	1p.2	+p.2	–	–	–
+ Alnetea	Plagiothecium ruthei							–	1p.2	+p.2	–	–	–
All. Scorpidion	Epilobium parviflorum							–	+r.1	+r.1	–	–	–
All. Scorpidion	Fissidens adiantoides							–	+p.2	–	–	–	–
+ Phragmitetea	Lycopus europaeus							–	+p.1	1p.1	+p.1	–	–
+ Molinietea	Atrichum undulatum							–	+p.2	–	–	–	–
All. Acrocl. phase	Peucedanum palustre							–	+r.1	1b.1	+r.1	+p.1	–
All. ,,	Acrocladium cuspidatum							–	+p.2	4a.4	+p.1	–	–
All. ,,	Brachythecium rutabulum							–	1p.2	2m.2	–	–	–
All. ,,	Lophocolea bidentata							–	–	2m.2	+p.2	–	–
All. ,,	Calliergon cordifolium							–	–	+p.2	+p.1	–	–
All. ,,	Brachythecium salebrosum							–	–	1p.2	–	–	–
+ Molinietea	Mnium undulatum							–	–	+r.2	–	–	–
+ ,,	Cardamine pratensis							–	–	+r.1	–	–	–
All. Sphagnion amb.	Sphagnum squarrosum							–	–	1a.3	4a.4	2a.2	4a.4
All. ,, ,,	,, fimbriatum							–	–	1b.2	3b.4	3a.4	2a.3
All. ,, ,,	Calypogeia trichomanis							–	–	2m.3	2m.3	+p.2	–
All. ,, ,,	Spagnum contortum							–	–	–	+p.2	–	–
All. ,, ,,	,, amblyphyllum							–	–	+p.2	2a.4	3a.4	+p.2
All. ,, ,,	Viola palustris							–	–	+r.1	+p.1	+p.1	–
Ass.	Dryopteris cristata							–	–	+p.2	+p.2	1b.2	+r.1
Ass.	,, carthusiana							–	–	+p.2	+p.2	1a.2	+p.2
All. ,, ,,	Spagnum teres								–	–	+p.2	2a.2	–
All. ,, pal.	,, palustre								–	–	1a.3	3a.3	3b.4
All. ,, ,,	Galerina paludosa								–	–	–	+p.1	+r.1
All. ,, ,,	Polytrichum commune var. uliginosum								–	–	–	2m.3	–
All. ,, ,,	Sphagnum papillosum								–	–	–	1p.2	–
All. ,, ,,	Aulacomnium palustre								–	–	–	1p.1–2	–
All. ,, ,,	Hierochloë odorata								–	–	–	1p.1	–
All. ,, ,,	Cephalozia bicuspidata								–	–	–	+r.2	–
All. ,, ,,	Dryopteris × uliginosa								–	–	–	+r.2	–
All. ,, ,,	Osmunda regalis								–	–	–	r.2	+r.2
All. ,, ,,	Mycena sanguinolenta								–	–	–	–	+r.1

TABLE 2 *(continued)*

		1	2	3	4	5	6	7	8	9	10	11	12
Species of the Alnetea glutinosae													
shrub layer (p.p. herb layer)													
	Alnus glutinosa juv.								+p.1	+r.1	+p.1	–	+a.2
	Salix cinerea juv.								–	+r.1	+r.1	+r.1	+p.1
	,, aurita juv.								–	–	+p.1	–	+b.2
	Frangula alnus juv.								–	–	–	+r.1	+b.2
	Betula pubescens juv.								–	–	–	+r.1	1b.2
	Myrica gale								–	–	–	–	2a.2
	Lonicera periclymenum								–	–	–	–	2a.2
	Rubus caesius × cf. scissus								–	–	–	–	+b.2
	,, gratus								–	–	–	–	+a.2
	,, scissus									–	–	–	+p.2
	,, cf. tereticaulis								–	–	–	–	+r.2
	Viburnum opulus								–	–	–	–	+r.1
Tree layer:													
	Alnus glutinosa								–	–	–	–	2a.2
	Betula pubescens								–	–	–	–	2a.1
	Quercus robur								–	–	–	–	+a.1
	Salix cinerea								–	–	–	–	+a.1
	Sorbus aucuparia								–	–	–	–	+a.1
Species of the Molinietea													
lFiipendulion	Calamagrostis canescens								2m.1	1p.2	1a.2	1a.2	+p.2
Magnocaricion	Carex paniculata								+ r.2	+ r.2	–	+p.2	+ r.2
Filipendulion	Lysimachia vulgaris								+p.1	+p.1	+r.1	1p.1	–
,,	Lythrum salicaria								+ r.1	+ r.1	+r.1	–	–
,,	Calystegia sepium								1a.1	+p.1	–	–	–
Cl.	Agrostis stolonifera								–	1p.2	–	–	–
+ Phragmitetea	Iris pseudacorus								–	–	+p.2	–	–
Magnocaricion	Carex acutiformis								–	–	+r.1	–	–
Cl.	Holcus lanatus								–	–	–	+p.2	–

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a number of species simultaneously. It is not intended to imply that this approach can replace the experimental investigation altogether. Generally speaking, the "actual" ecological amplitude (as observed under field conditions) is narrower than the physiological amplitude (as found in laboratory experiments; one might call this the "potential" ecological amplitude). In laboratory experiments many factors can be made to vary over a wider range than they do in nature, and certainly than they do in a fairly restricted area, and in addition the interdependence of various factors can be controlled more readily. However, in physiological experiments there is no selective pressure (such as competition, etc.). The imitation or simulation of natural conditions in an artificial culture medium also causes considerable difficulties, because usually one can not avoid excluding the interaction with certain constituents of the natural environment (such as the subsoil of an aequous medium, various other organisms, etc.), so that the establishment of a natural equilibrium can not be accomplished. Experimental research is of course also of extreme importance for the analysis of factors which can not be studied in the field or only scarcely so (such as photoperiodism), and also for investigation during unfavourable seasons, for taxonomic and genetic analysis of variance and, finally, for cytological (karyogenetic) examination.

Most scales used in ecological inquiry are linear, pH forming a notable exception. Conceivably the introduction of different, *i.e.* nonlinear scales, may offer considerable advantages especially for the recording of numerical data with appreciable ranges, such as the specific conductivity, and the chloride content in brackish waters, but also when the compounds often occur in very small quantities. A logarithmic scale, for instance, provides a higher degree of accuracy in concentrations lower than the basic number, whereas a greater precision in the higher concentrations is usually irrelevant, the factor in question being present in excess in any case. It is a question if the use of a logarithmic scale with the basic number 10 is always the most appropriate. It is, at least theoretically, possible that the basic number 2 or e (of the natural logarithms) may be more advantageous. (This is not a fundamental issue anyway, because the logarithms with a different basic number can be derived from each other by a simple multiplication by a constant). For a better insight in this matter it will be necessary to know more than we do at present about the manner in which the plants grow (e.g. by means of the dry weight yield) and about the various environmental factors. Conceivably a linear scale is not satisfactory in even a single instance.

The presence or absence of a species is of course not exclusively determined by chemical, physical or other environmental factors separately, but generally speaking certain biological laws decide its occurrence. The data recorded during the ecological studies in most cases do not provide a direct explanation of the reactions obtaining during the interaction between taxa and environment, and between individuals and species mutually. Every study of a biosystem ultimately leads up to an investigation of its production and of its energy balance.

5.1. *Structure and succession*

In open water with a mineral subsoil there is initially no shortage of nutrients. The pioneer vegetation is, as usual, of a simple structure and consists of a layer of elodeids. During our studies of water plant communities, also in other parts of this country and elsewhere in western Europe, a fixed sequence of life forms was observed, the stages consisting of rhizophytes preceding the stages containing pleustophytes. Roughly speaking, rhizophytes of low stature such as isoetids and *Charales*, are the forerunners of the taller rhizophyte vegetations containing, for instance, magnopotamids and, later on, nymphaeids (SEGAL, 1965). Which life forms follow each other successively depends to a large extent on the physical environment, the decisive factors being the dimensions of the mass of the water, and the horizontal and vertical currents.

The succession just mentioned is more particularly characteristic of stagnant water of peat pits, fen pools and lakes. In such waters marsh vegetations often develop either via a helophyte phase in places subject to the action of wind and wave wash, or via the submerse ceratophyllids succeeded by stratiotids and hydrocharids in the more sheltered places. The *Hydrochareto-Stratiotetum* presumably constitutes the structurally most highly organised community of aquatics occurring in Europe. The degree of organisation, expressing itself in the stratification and the variation of the life forms, is highest in fresh and eutrophic stagnant waters 1–2 metres deep, but it may be much less complicated in more extreme situations. In waters which have a very low nutrient content and in the excessively eutrophic waters, as well as in the waters of colder regions, in fast running streams, in larger or deeper masses of water, and in waters exhibiting appreciable fluctuations in certain environmental factors, exclusively vegetations of rhizophytes are found. In all intermediate situations linking these waters with the fresh, eutrophic, and calmer waters of average depths the structure of the vegetation usually becomes more complicated, and the velocity of the succession in the hydroseres also increases. Lemnids and ricciellids are characteristic of smaller areas of open water with dimensions not exceeding a few metres, and they thus often fill in the gaps between the floating leaves of *Hydrocharis* and the rosettes of *Stratiotes*, the space below them being occupied by the ceratophyllids *Utricularia vulgaris* or *Ceratophyllum demersum*.

The initial phases of the marsh communities developing out of the vegetations of hydrophytes are also richer in species when the succession started as a *Hydrochareto-Stratiotetum* than when it commenced as a helophyte interphase. Fairly soon at least one layer of low herbs and a well-developed bryophyte layer is present in addition to the helophytes. In a eutrophic environment ultimately alder carr develops, with a stratification of trees, shrubs, lianas, several layers of herbaceous plants, bryophytes, Fungi and epiphytic cryptograms. This more or less normal succession can result in an impoverishment of the environment, as is often the case in places where there is no longer a connection with open water, more particularly so when the water table has fallen, and also when the vegetation cover is continually removed by exploitation. This is manifest from the progressive simplification of the structure of the vegetation. However, *Sphagnum* vegetation, which is structurally very simple, is almost entirely lacking in the area under discussion.

5.2. *Topological and historical factors*

The far-reaching effects of dimensions and exposition have already been pointed out. The water level and the incidence of percolation phenomena are to a large extent determined by the relief of the landscape. Seepage is, generally speaking, concomitant with the following phenomena: In the winter season the water is a little warmer and in the summer somewhat colder than in corresponding places without percolation of water, in other words, the fluctuations in the temperature are less extreme. In winter no ice is formed over seepage areas or it is weaker there, more irregular or even bumpy. The water is commonly of a reddish brown colour and on the plants we find a rusty-brown deposit formed by the precipitation of iron compounds, in the first place ferric hydroxides and bicarbonates. The appreciable quantities of oxygen in the percolating water transform ferrous into ferric compounds. The surface of the water is often covered with a thin oily film containing iron bacteria. A common phenomenon is that the percolating water enriches the seepage areas in those waters which are by nature relatively poor in minerals, for instance by introducing dissolved calcium bicarbonate and other ions originating elsewhere and transported by the percolating water. On the other hand often there are considerable amounts of soluble iron compounds and these may eliminate nearly all the phosphate by precipitating them as insoluble iron phosphates. Seepage may occur intermittently and may be surprisingly localised. It is also dependent on the amount of rain fall, on the water economy (changes in the water table), and on the soil being more or less pervious to water which may, in its turn, be associated with the texture of the subsoil and the occurrence of more impervious soil layers.

Of paramount importance for the understanding of the vegetation is the recognition of the effect of human activities which have such far-reaching effects on the vegetation cover: inundation, drainage, control of the water level, desiccation, mowing, cutting, chopping down of trees and shrubs, burning, the application of manure and of fertilisers, peat digging, dredging, water navigation, pollution, wildfowl decoys, etc. It should be borne in mind that it is by no means always easy to retrace the past history of a certain area after the event.

5.3. *Chemical factors*

The results of our chemical analyses will be reported *in extenso* elsewhere. Only a few general remarks will be made here.

The composition of the open water is fairly constant. The absolute and the relative quantities of phosphate and of nitrogen are, as usual, rather low, but this does not preclude the possibility of available quantities of the essential elements (P and N) in the form of a constant replenishment from the mineral subsoil, or as ingestible organic compounds.

Differences between the soil and water present a difficult problem when considering the availability of nutrients to aquatic plants and especially rhizophytes. It is probable that the differences are not so great when the plants are rooted in the sapropelium layer or in soft peat as when the roots penetrate to the mineral soil beneath the organic deposits.

The inquiry into the relation between the chemical constitution of the water and the mineral subsoil is presumably more complicated as the subsoil is more solid, which is, among other things, related to the difference in absorption of ions on, *e.g.*, clay or loam particles. Clayey and loamy soils are relatively rich in calcium and potassium. A more thorough investigation is indicated. For the time being it is postulated that the chemical water analyses yield a certain amount of information concerning the nutrient requirements of the rooting plants, even if the ion relations in the water differ from those in the soil. The special significance of the buffering capacities of the soil in connection with the ion contents of the water is neglected.

It has already been pointed out that, especially through seepage and through periodic changes in the water level, and of course as a result of the intermittent development of a vegetation cover, the periodic fluctuations in the recorded environmental factors may be considerable. In this respect we have learned a great deal from taking the analyses of water samples, at various times of the year in the same spot. The fluctuations and variations proved to be highest in the phosphate content (it may differ by two orders), and furthermore in the ammonium, sulphate and calcium contents.

In the course of the succession in seepage areas the general trend is a gradual decrease in the specific conductivity, in pH, in the hardness and bicarbonate concentration, and in the chloride and calcium content, and an increase in the organic ammonium and phosphate, only the sulphate content showing a "peak" in the *Pellia* phase, all this in spite of the fact that generally speaking percolated water enriches the environment and normally causes a local increase in the specific conductivity, in the pH values, in the hardness, and in the chloride, bicarbonate, ammonium, iron and calcium concentrations, accompanied by a decrease in the phosphate and the sulphate content.

6. Geographical comparison of peat-bog and fen vegetations in Europe

A comparative study of the literature on peat-bog and fen vegetation, more particularly of publications pertaining to the so-called "*Zwischenmoore*", reveals that a considerable number of records reported in these papers cannot be used because the bryophyte layer is either not taken into consideration at all, or only incompletely so, or the constituent species have not been correctly named. For an exhaustive description and characterisation of these vegetation types, for both floristic and ecological purposes, the composition of the moss and liverwort layer is of special significance, and in several respects even more important than the herb stratum. One should bear in mind that the bryophyte layer covers a considerable portion of the soil surface (it is frequently even completely closed), and that many mosses are much better habitat indicators than higher plants.

My own studies of hydroseres in fen and peat-bog country outside the Netherlands indicate that the resemblance in the sequence of the respective stages is striking. In more alkaline and more continental marshes parallel series occur, with ecologically or geographically differential species occurring in the consecutive phases, as compared to the Dutch bog and fen vegetations. We find, for instance, in the *Scorpidium* phase *Riccardia sinuata*, *Drepanocladus exannulatus* and optimally *D. intermedius*, in the *Pellia* phase *Pellia endiviaefolia*, *Bryum ovatum* and *Mnium seligeri*, in the *Sphagnum amblyphyllum* phase *Sphagnum subsecundum*, *Paludella squarrosa*, *Helodium blandowii* and *Calypogeia fissa*, in the *Sphagnum palustre* phase *Tomenthypnum nitens*. Differential species of the herbaceous layer are, *e.g.*, *Epipactis palustris*, *Crepis paludosa*, *Selinum carvifolia*, *Carex lepidocarpa* and *C. flava*. *Carex diandra* or *C. lasiocarpa* can be replaced by *C. limosa*, especially in *lagg* zones. In Poland the "*Myricetum*" is partly replaced by the "*Saliceto-Betuletum humilis*" with *e.g.*, *Salix rosmarinifolia*, and in at least the western Alps by the "*Salicetum arbusculae*", in which occur, apart from *Salix arbuscula*, also *S. caesia* and *S. glauca*, with, in limestone areas, also *S. hastata* and *Listera ovata* (Segal, 1963). The occurrence of vicarious species in these parallel seres is most remarkable. The succession line can be continued to the ombrogenous high moor peat-bogs on the one hand, with *e.g.*, *Drepanocladus fluitans*, *Calliergon stramineum*, *Calypogeia sphagnicola* and a considerably number of *Sphagnum* species, and to the more eutrophic seres on the other, with *Drepanocladus aduncus*, *Riccia fluitans*, *Campylium polygamum*, *Calliergon cordifolium*, *Pallavicinia lyellii* as the opposite numbers of *Pellia* species, and *Chiloscyphus polyanthus* as the replacement of *Calypogeia* species. Also in higher plants corresponding vicariads can be observed very clearly, *e.g.*, between species of *Eriophorum*, *Dactylorchis* and the *Carex flava* aggr., but also between *e.g.* *Peucedanum palustre* and *Selinum carvifolia*. In the case of *Eriophorum* the vicariad series runs as follows: *E. vaginatum* in ombrogenous high moor peat-bogs, *E. gracile* in the not quite so acid fen bogs, and *E. latifolium* in somewhat more alkaline peat marshes, whereas *E. angustifolium* has a much wider range of tolerance.

A fifth type of peat-bog, that of the *lagg* zones, must be left out of consideration, but it is noteworthy that in this case also a number of vicariating species are characteristic.

In general, *Drepanocladus* species are particularly suited as habitat indicators. One of the species not mentioned previously, *D. revolvens*, is most probably typical of contact situations between oligotrophic peat-bogs and a more alkaline subsoil.

7. Discussion

If one attempts to classify the marsh vegetations discussed in this paper, it proves to be almost impossible to apply an ordination system even in a relatively small area. There are too many factors that are operative simultaneously and are, at the same time, correlated to a larger or lesser extent. In contradistinction to what one might expect from the numerous papers on the subject, classification is not so easy either.

In these vegetation types the absence of clear-cut discontinuities is a great handicap. Continuity in the succession can be observed both in space and in time. The "locosynclines" are the result of a complex ecosyncline, gradients being demonstrable in the setting and raising of the humus deposits, in the relative lowering of the ground water level, in the decreasing quantities of essential mineral nutrients (and the lowering of the specific conductivity), and in the pH ranges. In a geographical sense, however, other ecosynclines, toposynclines, and "oreosynclines" play a part. An interesting example of an oreosyncline was reported by Oberdorfer (1957) when he described, within the "Assoziationsgruppe der *Schoenus*-Moore", the *Orchido-Schoenetum* of the lower regions ("Tieflagen"), the *Primulo-Schoenetum* of the submontane to montane zones, and the *Schoenetum subalpinum* of the higher montane to subalpine habitats. These three vegetation types may be in direct contact.

The description of "associations" in marsh regions according to objective standards is hardly possible. One may wonder whether it is advisable to avoid describing associations altogether.

Perhaps it is only permissible to distinguish higher synsystematic units, with the exception of vegetation types of the more extreme habitats, *e.g.* those of northern Scandinavia.

In any event it can scarcely be maintained that the systematic classification should be based almost exclusively on the higher plants, as is the custom. It seems advisable to recognise, apart from the conventional classification in the *Rhynchosporion albae* (Koch, 1926) of the *lagg* zones, the *Caricion davallianae* (Klika, 1934) or *Eriophorion latifolii* (Braun-Blanquet & Tüxen, 1943) of the more alkaline fen bogs, the *Caricion lasiocarpae* (Vanden Berghen, 1949) or *Eriophorion gracilis* (Preising apud Oberdorfer, 1957) of the more acid bogs and the *Caricion canescentis-fuscae* (Nordhagen, 1936), differences between vegetations of the various succession-stages. One might consider distinguishing alliances in the nature of a *Scorpidion* (Du Rietz,

1949) (or perhaps better: a *Campylio-Drepanocladion*), *Sphagnion amblyphylli* and *Sphagnion palustris*. This last alliance is more or less identical with the classical *Caricion canescentis-fuscae*. Within each of these alliances a number of vegetation types is characteristic. Such a classification does not coincide at all with vegetation units previously recognised in other systems of classification, such as the *Schoenion ferruginei* (NORDHAGEN, 1936). Possibly also the *Acrocladium* vegetations should be given a place in this system. *Sphagnum recurvum* vegetation types occupy a place of their own. When this species occurs in large numbers, it is usually indicative of a disturbance in the natural succession, such as the influence of a light dunging or another form of pollution, or the gathering of peat moss for horticultural uses. This may conceivably provide the explanation of the very high abundance of *S. recurvum* in the uppermost layers of peat profiles deposited in historical times. This phenomenon has been described by, *e.g.*, PEARSON & GREEN (1964).

Before a permanent solution to the problem of classifying marsh vegetation is reached, a good deal of study throughout Europe is required.

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