ON THE ECOLOGY OF A SPHAGNUM BOG

by

Members of the Leidsche Biologen Club

communicated by

L. G. M. BAAS BECKING and Miss E. NICOLAI.

(Leiden)

Statement of the problem.

For the ecologist systematic units are actors in a play. Whatever their christian- and family-names may be — it is their role, whether master or servant, whether villain or hero — which determines the character of the performance. This performance has, moreover, the property of being both continuous and simultaneous: all scenes are given at once. Such a continuous and simultaneous performance is called a *biocoenosis.*

In a great many ways, a biocoenosis reminds us of an organism. For the coördination between organs or tissues, or even cells is also continuous and simultaneous. A biocoenosis is a higher vital unit, and may be approached by the same methods which we use for the study of organisms (v. D. KLAAUW (24)). In the systematic approach we establish the name, sex and age of the actors, in the anatomical approach the "pattern" of the constitutional units is established ("the dramatical situation"), while the physiological approach is concerned with the metabolism of the entity ("the plot"). As counterpart of these methods. however, we have to consider the study of the environment. The environment, which LOTKA has called "the stage of the life drama" (28).

This environment may be analyzed, and its various factors recorded. A synthetic picture of the environment, the *milieu,* should be the common denominator of the potentialities of the organisms which constitute the biocoenosis.

Our colleague, Professor LAM, has emphazised, in his inaugural address (27) the fact that a taxonomical study "per se", without a stimulus from allied fields of science, such as Geology, Genetics and Ecology, may yield less satisfaction to the investigator than work plotted in coordination with the related disciplines. This attitude encouraged us to report in this issue upon the results of an Excursion of the „LEYDEN BIOLOGISTS CLUB'', held in the autumn of 1932 to a high-moor region in Drenthe.

Although none of the participants were ecologists and most of the results obtained were well-known in the literature, several of us have derived a stimulus from the field-observations which gave a fresh impetus for laboratory work. And regardless of the fact that men like GAMS (13, 14), HARNISCH (21), KOTILAINEN (25) and in our country W. BEIJERINCK (7) did give us synthetic pictures of the high-moor biocoenosis, the experience we obtained was our own, the methods of approach were, in part, different from the others and while we only spent a few days in the field, our group included several persons. As an instantaneous picture, therefore, our survey may have some significance.

In order to use the available time efficiently our study was centered upon a small highmoor pond, and after a preliminary topographical survey the character of its vegetation, of its water and of the climatological conditions was established.

The following members of the „LEIDSCHE BIOLOGEN CLUB'' took part in the work: MISSES T. HOF, A. VAN OVEN, A. KRIJTHE, E. BEER, S. HASPERS, R. BOK and J. DE ZEEUW and Messrs. K. VAAS, H. VERDAM, CH. NASS and W. KARSTENS. Dr W. BEIJERINCK, Director of the Biological Station at Wijster, Drenthe, has given much help and advice. Without his collaboration the work would have been impossible.

D. F. 7, named in Dr W. BEIJERINCK's work (6), is an almost circular pond, situated in a slight depression in an open heather, halfway between Wijster and Spier. The diameter is 75—85 meters, the maximum depth is 2.2 meters, the area 0.6 Hectare (see Fig. 1). The heather slopes gently towards the N.W., and it seems that the bog drains in this direction. The Western part is covered by an almost closed cover of *Sphagnum medium* LIMPRICHT, in which there are many ''kopjes'' of *Calluna* and *Molinia*. The Eastern part is chiefly open water with islands of *Carex inflata* and *Calluna* + *Molinia*, partly with a sandy bottom.

The bog-ore stratum does not fully extend under the pond, the bottom sand, however, is almost stony-hard and seems quite impervious. The N.E. shore is steep and shows the effect of water erosion. The prevailing winds are S.W. As may be seen from the block-diagrams (Fig. 2),

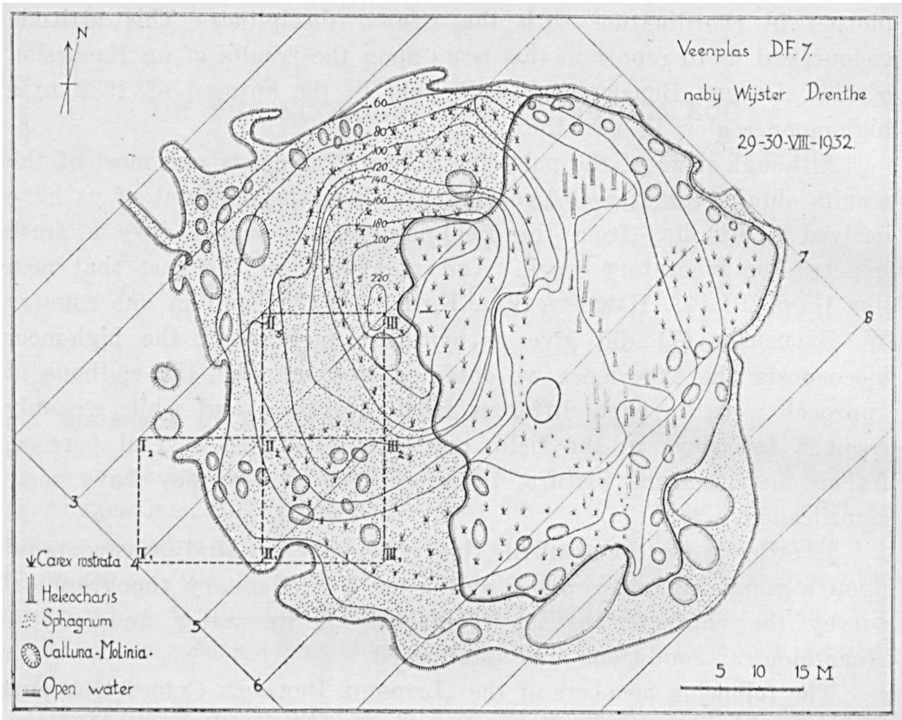
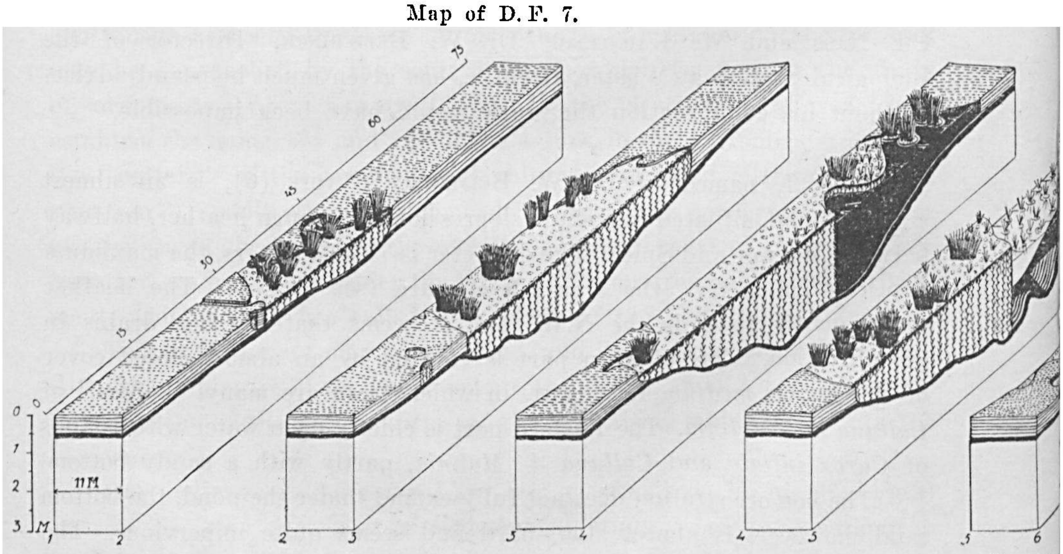


Figure I.

Map of D. F. 7.



Figure

Block diagram

Legend as in

in which the bog is devided in to eight "Meter-blocks", running S.W. to N.E., the Sphagnum forms more than 2 M. deep masses. In the centre of the pool curious ripples exist on the bottom.

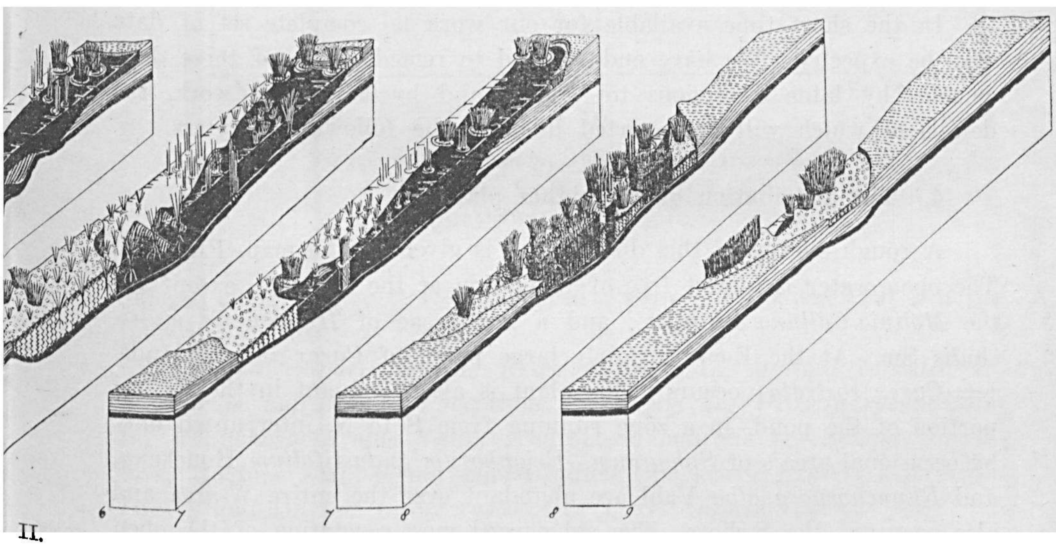
The character of the pond is that of an ombrogenic high-moor pond of the "Solle" type (according to the nomenclature of the German phytogeographers).

Methods of approach.

The pool does not represent a closed community. Possibly there are no exclusive biocoenoses on this earth because, even in the deepest mines, there is constant infection from the atmosfere, which carries a great amount of animated matter in the form of spores and cysts.* Motile organisms may also carry seeds and spores; birds, lizards and insects may cause a wide distribution of plants in the heather. The characteristic community will develop in spite of the "exposed" topography by the exclusiveness of its milieu, and therefore the factors of this milieu have to be analysed.

In ecological surveys much stress has been laid upon an accurate inventarisation of the existing organisms. While such a survey is, of

* The occurrence of the common Stickleback (*Gasterosteus aculeatus*) in D. F. 7 has remained a puzzle to us.



II.
of D. F. 7.
Figure I.

course, very pertinent to a possible understanding of a vital community, it seems remarkable that the environmental factors (despite the perfection of the methods by which they may be determined) are, in many cases, neglected. By selecting a small area for our investigation the survey could be sufficiently restricted to allow for sufficient time to be devoted to environmental factors. Our survey was therefore specified as follows:

1. Topography.
2. Land animals (Investigated by Dr H. BLÖTE and a group of students. Miss A. M. BUITENDIJK (11) found two species of Collembola as new for the Dutch fauna: *Deuterosminthurus insignis* (Reut.) and *Deuterosminthurus novemlineatus* (Tullb.). Other results are as yet not available.
3. Aquatic animals (Investigated by Prof. Dr H. BOSCHMA and a group of students. Results as yet not available).
4. Higher plants.
5. Algae.
6. Microbes.
7. Mineral environment; dissolved substances and gases.
8. Acidity.
9. Temperature and humidity.
10. Pollen analysis of different strata.

In the short time available for our work no complete set of data may be expected. We have endeavoured to remedy some of these deficiencies by later excursions to Wijster and by laboratory work, the details of which will be reported upon in the following chapters.

4. The distribution of the higher plants.

A rough survey of this distribution is given on the map, Figure 1. The open water is almost free of vegetation at the N-E-end, except for the *Molinia-Calluna* "kopjes" and a few areae of *Heleocharis multicaulis* Sm. At the E-end a fairly large patch of *Carex inflata* Huds. (= *Carex rostrata*) occurs. This plant is also dominant in the central portion of the pond, in a zône running from S to N, interrupted only by occasional area's of *Sphagnum*. *Eriophorum angustifolium* Honckeny, and *Rhynchospora alba* Vahl are abundant over the entire W-area and also occur at the S-shore. The submerged moss-vegetation of the open water consists almost entirely of *Lophozia inflata* var. *laxa* and of *Sphagnum recurvum* P. d. B., as already mentioned by Dr W. BEIJERINCK in his survey of 1926. It seems that the nature of the pond has not changed much in the last six years; possibly the pond has assumed a slightly less oligotrophic character, which also appears from the algal flora.

A more detailed survey was made of a few selected 30 ft traverses at the S-W end of the pond (see Fig. 3) where 4 × 30 square feet were

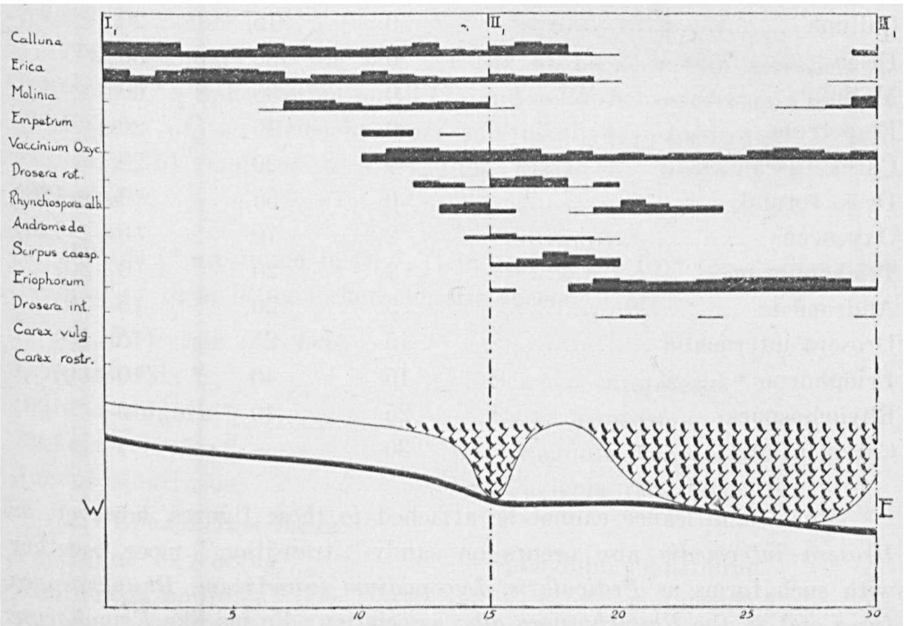


Figure III.

Frequence of different species on a traverse.
S—E at the S—W and of D. F. 7.
As shown in Figure I.

indexed on frequency ("Deckungsgrad", see e.g. MARKGRAF [29]) of the following species:

Calluna vulgaris Salisb., *Erica Tetralix* L., *Molinia coerulea* L., *Empetrum nigrum* L., *Vaccinium oxycoccum* L., *Drosera rotundifolia* L., *Rhynchospora alba* Vahl., *Andromeda polifolia* L., *Scirpus caespitosus* Hartm., *Eriophorum angustifolium* Honckeny, *Drosera intermedia* Dreves and Hayne, *Carex fusca* All., *Carex inflata* Huds.

The profiles I, II and III, show frequency and topography, *Calluno-Molinietum Sphagnetum* on the traverse with a "kopje" near II.

The appearance of the different components as a function of depth of the moor is striking. This also appears from the other W—E and the two S—N profiles (see Fig. 2).

Averaging the results of 120 square feet it appears that the various species may be classed as follows:

	Depth of bog (in cm.)		
	Minimum.	Average.	Maximum.
Calluna	0	15	20
Erica	0	30	60
Molinia	0	35	60
Empetrum	0	10	20
Carex fusca	0	20	20
Dros. rotund.	0	55	(0—>120)
Oxycoccus	2	70	(0—>120)
Trichophorum	3	20	(0—30)
Andromeda	5	20	(5—30)
Drosera intermedia	15	25	(10—30)
Eriophorum	15	40	(10—60)
Rhynchospora	25	40	(10—>100)
Carex inflata	30	—	>120

Much significance cannot be attached to these figures, however, as *Drosera intermedia* also occurs on sandy "transition" moor together with such forms as *Pedicularis, Lycopodium inundatum, Rhynchospora fusca* etc., in the *Rhynchospora alba* association. Forms like *Eriophorum angustifolium* also thrive on a solid soil. *Carex inflata* seems, in many cases, actually to reach the soil in very deep Sphagneta. Various *Carex* plants were dug up, and down to a depth of 120 cM., the roots seemed to reach the bottom. The same was the case with *Heleocharis* which, however, prefers open water and needs the contact for anchoring. In the case of the *Carex* it might be that the plants actually derived other benefit from the substratum (see also Pond [38]).

As the pH of the water in the entire "basin" amounted to 4 (see later) we might expect eury-oxyphilous to eury-mesoionic plants according to the Swedish classification (see Gams and Ruoff [17]). It seems, however, that the occurrence does not seem to fit in this scheme, according to which this plant should occur in environment with pH 5—6.5 (steno-meroionic). Gams himself points out this discrepancy in a later paper (Gams [16]). The great influence of pH upon the distribution of plants cannot be denied (GUSTAFSON [20], ARRHENIUS [2]) but it seems that a rigid classification, based on pH *only*, may not account for the distribution of a group of plants which belong to the same biocoenosis. Root-structure, anaerobiosis, nature and depth of the substratum may all be factors that control a distribution.

According to Dr W. C. DE LEEUW there are indications that the following plant communities are present according to the system of BRAUN BLANQUET (10).

The boundary of the bog consists of an Ericetum tetralicis (1) followed by a Sphagnetum medii (2) and a Rhynchosporetum albae (3). Fragments of a Heleocharetum multicaulis (4) Caricetum inflato-vesicariae (5) and of a Caricetum fuscae (6) probably are also represented.

Plants (* are found in D. F. 7) indicating the first three associations (several of them being "characteristic species") are:

1. *Ericetum tetralicis.*

Erica tetralix *	Scirpus caespitosus *
Calluna vulgaris *	Carex panicea
Molinia coerulea *	Sphagnum compactum
Juncus squarrosus	(Cladonia rangiferina *)

2. *Sphagnetum medii.*

Vaccinium oxycoccus *	Sphagnum acutifolium
Andromeda polifolia *	„ molluscum *
Drosera rotundifolia *	„ recurvum *
Empetrum nigrum *	Aulacomnium palustre *
Eriophorum vaginatum *	Polytrichum commune
Sphagnum medium *	„ strictum
„ rubellum *	

3. *Rhynchosporetum albae.*

Rhynchospora alba *	Rhynchospora fusca
Drosera intermedia *	Zygogonium ericetorum
Eriophorum angustifolium *	Sphagnum recurvum *
Lycopodium inundatum	„ cuspidatum

The fragments 4), 5) and 6) all belong to a more eutrophic flora.

5. The Algae.

An unusual algal flora should be expected in the acid water of the high-moor bog DF 7.

BEIJERINCK (7) has investigated the flora and fauna of a great many peat bogs on the high-moor of Drenthe including DF 7. It seemed worth while to reexamine the flora for possible changes between the years 1927 and 1932.

The following samples were taken of the plankton of the peat bog on the afternoon of August, 30th;

three samples from the open water,

one of sqeezed-out *Sphagnum cuspidatum* growing in a depression near the Callunetum,

one of sqeezed-out *Sphagnum magellanicum* on a "kopje" near the Callunetum and one of sqeezed-out *Leucobryum* and *Sphagnum rubellum.*

The examination could not be undertaken on the spot, except for a few preliminary observations. Further examination was made on formalin-material by Mr. K. VAAS. Due to this fixation most of the Flagellates became irrecognizable.

In the following list of species those observed by BEIJERINCK (1927) are marked with B, those by VAAS (1932) by V.

TABLE I.

Algae of DF 7.

Flagellatae.		
Spongemonas. uvella	B	
Rhipidomonas Huxleyi	B	
Mallomonas caudata	B	
Synura uvella	B	V
Dinobryon divergens	B	V
Cryptomonas ovata	B	
Trachelomonas volvocina	B	
Goniostomum semen	B	
Glenodinium uliginosum	B	
Peridinium cinctum. var. palustre	B	V
„ inconspicuum	B	V
„ lubiniense	B	
,, minusculum	B	
„ pusillum	B	
Chlorophyceae.		
Asterococcus superbus	B	V
Oocystis solitaria	B	
Tetraedron enorme	B	

Binuclearia tatrana	B	
Microspora floccosa	B	
„ tumidula	B	V
„ spec. div.	B	V
Oedogonium Itzigsohni	B	V
„ spec. div.	B	V
Zygogonium ericetorum	B	
Mougeotia spec. div.	B	V
Spirotaenia fusiformis	B	
Cylindrocystis Brebissonii	B	
Penium spirostriolatum	B	V
Netrium digitus	B	V
Closterium acutum var. Linea	B	
„ Jenneri	B	
„ juncidum		V
„ Ulna	B	V
Tetmemorus Brebissonii v. minor.	B	V
Euastrum binale. div.	B	V
Micrasterias truncata	B	V
Cosmarium amoenum	B	
„ Cucurbita	B	V
„ Portianum	B	
„ pygmaeum	B	
„ pyramidatum	B	
„ subtumidum	B	V
„ trachypleurum minus	B	
Xanthidium antilopaeum	B	
Arthrodesmus incus	B	
„ octocornis	B	V
„ Brebissonii	B	
„ dejectum	B	V
Staurastrum furcatum	B	V
„ margaritateum	B	V
„ paradoxum	B	V
„ polymorphum	B	
„ teliferum	B	
Hyalotheca dissiliens		V
Gymnozyga moniliforme	B	V
Spondylosium pulchellum	B	V

Heterocontae.		
Botryococcus Brownii	B	
Baccillariales.		
Tabellaria flocculosa	B	
Eunotia Arcus	B	
„ gracilis	B	
Navicula Rhomboides	B	V
Pinnularia linearis	B	V
Nitzschia gracilis	B	
Cyanophyceae.		
Chroococcus turgidus		V
Hapalosyphon hibernicus	B	V
Aphanizomenon flos aquae	B	V
Microchaete tenera	B	

A great many common filamentous algae (*Cladophora, Vaucheria Spirogyra*) do not occur in the water of the peat bog. The absence of those algae is due to the acid nature of the water and to its dearth in Calcium. Many of the blue-algae have a brownish colour, as already described by GEITLER (18) for similar localities.

The plankton of the open water contains the greater part of the filamentous algae, whereas the Desmidiacea and especially their smaller forms occur in the samples of sqeezed-out *Sphagnum.*

It stands to reason that the amount of species observed by VAAS is a great deal smaller than the list given by BEIJERINCK because of the limited material at our disposal. The more striking is the fact that VAAS has found a few species that did not occur in DF 7 in 1927, the year when it was examined by BEIJERINCK.

Under those forms we mention *Hyalotheca dissiliens* (Smith) Bréb., *Closterium juncidum* Ralfs, *Chroococcus turgidus* (Kütz) Näg.

The last form also occurs in a near-by pond, so that its area might very well have been extended in the last few years.

Hyalotheca dissiliens was also found by one of us on the reexamination of the natural environment in the autumn of 1932. On this occasion *Cosmarium sphagnicolum* and *Closterium linearis* were also added to the list. The algal flora seems to have increased in the last five years.

6. The Microbes.

The high actual acidity precluded the existance of many forms that ordinarily occur in natural waters. The investigations of VAN NIEL (32) for example, show that purple and green bacteria cannot thrive in acid waters; the same is true for *Cytophaga hutchinsonii,* which attacks cellulose, and of *Azotobacter chroococcum,* which form fixes atmospheric nitrogen and *Bacillus stutzeri,* a denitrifyer.

Other forms like *Aspergillus, Phycomyces* and the *Thiobacillus thiooxydans,* forms either adapted to a high acidity or ubiquitous organisms, might very well occur in the high-moor bogs.

Apart from such predictions, field observations already show evidence of well developed microbial life. The presence of methane and sulphuretted hydrogen for instance point to bacterial activity.

As far as the literature is concerned there are very few helpful statements as to the presence of specific organisms, apart from the work on humus-fungi carried out by OUDEMANS and his collaborators (33).

WAKSMAN (46) who has made an intensive survey of microbial activity in peat-bogs, seems to be chiefly interested in decomposition of plant-remains, both aerobically and anaerobically, and does not describe specific forms.

RITTER (39) mentions the occurrence of butyric acid fermentation in the bogs caused by typical *Clostridia.*

SCHLÖSSING (40) observed the disappearance of methane when the cultures were infected with heather-soil.

Evidence of bacterial activity as shown by the presence of volatile acids will be discussed later in this paper.

Dr W. BEIJERINCK demonstrated the presence of bacteria in the air-cells of *Sphagnum cymbifolium* and Miss A. VAN OVEN corroborated this fact. It seems, therefore, that a copious bacterial flora exists in peat-bogs and a more detailed investigation was desirable. This investigation has to be considered, however, as a preliminary survey.

Samples of bog-water were collected in evacuated soft-glass tubes drawn out to a fine point, which point was heated in a flame before immersion. After immersion the point was broken off and the filled tube sealed with Sphagnum as the "Primus-burner" did not give sufficient heat to seal the tube.

Mud from the bottom of the peat-bog and different species of Sphagnum were collected in sterilized bottles.

A direct survey of the microbes was only possible in the above mentioned case of Sphagnum-plants.

For further investigation of the bacterial flora, carried out by Miss A. VAN OVEN, the samples were inoculated in various culture-fluids.

Those fluids were intended to give the optimum conditions for the growth of different species of bacteria, in order to obtain an accumulation of these special bacteria.

Two series of each culture-fluid were examined, one having the original composition as cited in the literature, the other similar to the former but adjusted to a pH of 4.

The following species of bacteria could be obtained:

a. *denitrifying bacteria,* isolated in a medium used by ELEMA (13) containing 2 % glycerol and 0.5 % KNO_3, buffered to pH 4 by means of citric acid. Under anaerobic conditions development of gas could be observed within a week.

Gas- and bacterial development proved to be more copious in the cultures adjusted to pH 4.

The gas proved to be a mixture of carbon dioxyde, oxygen and nitrogen. A pure-culture on peptone-agar showed white colonies of rod-shaped Gram-negative bacteria, 1—4 μ in length.

b. *aerobic thiobacteria,* cultivated in a solution indicated by KÜSTER (26) containing $Na_2S_2O_3$, $NaHCO_3$, NH_4Cl and $MgCl_2$; one series buffered to pH 4, the other by means of K_2HPO_4 to pH 5.4.

The aerobic cultures showed a marked development of bacteria indicated by the production of sulphur.

In this case too the culture-fluid adjusted to pH 4 showed a more copious development of the microbes.

Pure-cultures on peptone-agar and microscopical investigation showed no difference whatever between those forms and the denitrifying bacteria. It seemed justified to try the aerobic Thiobacteria on denitrifying power in anaerobic cultures and vice-versa.

Those cultures succeeded, so probably both processes are due to the action of one and the same organism.

A further investigation on this subject was carried out by Miss T. HOF in the Microbiological Laboratory at Delft. *

Miss HOF inoculated the Thiobacteria from a pure culture on

* The Director of this Institute, Prof. Dr A. KLUYVER, has given us much helpful assistance.

peptone-agar in a medium described by BEIJERINCK (5) containing $Na_2S_2O_3$, $NaHCO_3$, NH_4Cl, $MgCl_2$ and KH_2PO_4 instead of K_2HPO_4; adjusted to a pH of 4 by means of phosforic acid. The decomposition of thiosulphate was controlled by titration with iodine; after six days a disappearance of thiosulphate could be observed; the pH increased from 4 to 8. In the fluid neither sulphate nor sulphur were formed.

Very likely the following reaction takes place:

$$2\,Na_2S_2O_3 + O + H_2O = Na_2S_4O_6 + 2\,NaOH$$

In this case the increasing pH is due to the formation of NaOH.

The various reactions obtained with the Thiobacillus of Wijster showed a marked resemblance with forms described by TRAUTWEIN (46).

Therefore the bacteria were cultured in the medium as given by TRAUTWEIN ($Na_2S_2O_3$, $NaHCO_3$, NH_4Cl, $MgCl_2$, K_2HPO_4) but adjusted to a lower pH by replacing K_2HPO_4 by KH_2PO_4 and by addition of phosforic acid.

In the fluid adjusted to pH 4 no growth of bacteria took place; in a fluid of pH 5.5 the bacteria developed well as was shown by the fact that within two weeks the whole amount of thiosulphate had disappeared and the pH increased from 5.5 to 8.

The only difference with TRAUTWEIN's Thiobacillus seems to be that the latter causes the formation of tetrathionate and of sulphate, whereas the Thiobacillus of Wijster does not produce sulphate in the fluid.

The production of polythionates could be proved by addition of bromine to the culture-fluid which caused the formation of sulphate.

TRAUTWEIN's Thiobacillus causes denitrification both under autotrophic and under heterotrophic conditions (47), whereas Miss HOF tried in vain to obtain denitrification with the Thiobacillus of Wijster.

Considering the fact that Miss VAN OVEN obtained denitrification with the same bacteria in the same media, the different observation might be explained by a loss of the faculty of denitrification caused by prolonged culture on peptone-agar. BEIJERINCK (6) described a similar case: bacteria which caused denitrification with Sulphur as a source of energy lost this faculty after culture on organic media.

In this case no further observations have been made and the question remains open whether the Thiobacillus of Wijster is able to cause denitrification.

In any case the form seems to be related to TRAUTWEIN's Thiobacillus (46).

c. *Sulphate-reducing bacteria* developed only in the cultures inoculated with bottom-mud from the bog. After two weeks the culture-fluid of BAARS (3) became black by the formation of PbS.

The cultures inoculated by samples of bog water showed no such development of bacteria whereas in a few cases the inoculation with Sphagnum plants gave a development of bacteria after 4 weeks.

The bacteria observed were Spirillae and rod-shaped bacteria; pure cultures did not succeed.

d. *Butyric-acid bacteria* developed abundantly from mud, water and Sphagnum-inoculations under anaerobic conditions; the media contained glucose and fibrin or soluble starch and fibrin.

Microscopical examination showed plectridia about 4 μ in length.

In the solutions buffered to pH 4.3 the bacteria caused a slight increase of the pH to about 4.5; in cultures with an initial pH of 7 a decrease occurred down to pH 4.5.

The butyric-acid bacteria seem to form an important part of the microbiological flora of the peat-bog, as was observed already by RITTER (39).

As to the occurrence of cellulose-decomposing bacteria no definite observations have been made. Only in one case a slight decomposition of cellulose could be observed. In this case 1 gram of straw and 5 cc. of a sample (mud or water) were added to a solution according to WAKSMAN (50), containing $(NH_4)_2PO_4$, $MgSO_4$, KCl and K_2HPO_4. Cultures both under aerobic and anaerobic conditions showed a beginning of decomposition after three months. Small rod-shaped bacteria were present.

Examination of the water and mud of the peat-bog on the presence of Fungi was carried out by inoculation on prune-agar buffered to pH 4. A Fungus developed and could be classified by the Central Bureau of Fungus Cultures at Baarn as *Syncephalastrum cinereum* Bainier.

7. The environment.

Mineral environment and gases.

One of the most striking characteristics of high-moor bogs is the oligotrophic character, the dearth in mineral substances. The following analysis of the water of DF 6, a peat-bog near to DF 7, carried out by the Central Bureau of Hygiene in the spring of 1926 is a sufficient proof of this fact.

TABLE II.

Free carbon dioxide	6.1	mgr/litre
Fe_2O_3	0.1	"
CaO	3.3	"
MgO	3.0	"
P_2O_5	0	"
K_2O	0	"
Cl^-	12	"
Total amount of nitrogen	1.6	"
Oxygen consuming capacity	7.4	"
Free oxygen	10.5	"
Temperature during the determination of the oxygen ...	14.5° C.	

DF 7 belongs to the typical high-moor bogs which probably do not communicate with the ground-water, therefore its mineral composition depends entirely on the rain-fall. In relation to this fact it seemed interesting to obtain an analysis of the rainwater. This analysis was made by the "Government Bureau of Water Supply" (Rijksbureau voor Drinkwatervoorziening) of a sample taken in the spring of 1933.

TABLE III.

Conductivity at 18° C. $\times 10^6$	29	
Cl^-	4.9	mgr/litre
NO_2^-	0	"
NO_3^-	0	"
$SO_4^=$	7.5	"
Ca	3.3	"
Ca as CaO	4.6	"
Mg	0.7	"
MgO	1.2	"
Na	4.9	"
Total hardness	0.63	

During the excursion the chemical survey of the bog-water was limited to the analyses of oxygen, carbon-dioxide and sulphuretted hydrogen.

The presence of volatile organic acids was examined in the laboratory at Leyden.

The amount of dissolved oxygen was determined by the original method of WINKLER (54), the samples have to be collected with great care in order to avoid the entrance of air-bubbles into the bottle. Therefore the sample bottle was connected with an aspirator; by applying suction to the outlet of this aspirator the water was flushed through the sample bottle into the aspirator.

To the samples were added successively manganous sulphate, alkaline potassium iodide solution and sulphuric acid. The iodine set free is a measure for the amount of dissolved oxygen and may be titrated easily with a solution of sodium thiosulphate.

The results were expressed in percentage of saturation by using a graph in which the correlation between oxygen in mgr/litre and temperature of the sample is given.

It was dubious whether this method could give the exact amount of oxygen in the sample because of the presence of organic matter in the water; and above all the relatively large amount of sulphuretted hydrogen appeared as a source of errors.

In order to avoid those errors the samples were treated at first with concentrated sulphuric acid and a potassium permanganate solution, as indicated in the "Standard methods for the Examination of Water and Sewage" (45).

As the last method gave very uncertain results and as many objections were made to it (ALSTERBERG [1]), the results obtained by the original WINKLER method seemed preferable with the restriction that the results should be a little too high.

In the literature the dearth of oxygen is considered as one of the characteristics of the peat-bogs (PEUS [37]). HARNISCH (21) observes that in small bogs when the water is not disturbed a total lack of oxygen occurs, whereas in larger bogs the surface is stirred by the wind and may contain a considerable amount of oxygen. For our small pond one could expect a low saturation value. This prediction proved to be true. Two samples were collected at two localities; in the open water and in a depression of the Sphagnetum where the greatest changes were bound to occur in connection with photosynthesis; at the same time water from the surface and from a deeper layer (10—20 cm below the surface) was sampled.

The percentage of saturation was small, the highest amount in the Sphagnetum being 20 %, in the open water 93 %. A rapid decrease was observed in the deeper layers.

Figure 4 shows the variation in oxygen-saturation of a depression in the Sphagnetum during a day and a night, the samples being taken at 1 cm. and at 10 cm. below the surface.

It may be seen that the amounts of oxygen increase in the surface water during the morning and that a maximum occurs between 13 and 15 hours, followed by a rapid decrease and a minimum at midnight.

The difference between surface and deeper layers needs no further explanation.

It proved to be interesting to compare those results with the data obtained for the amount of sulphuretted hydrogen (as shown in the same Figure). Sulphuretted hydrogen was determined by adding to the

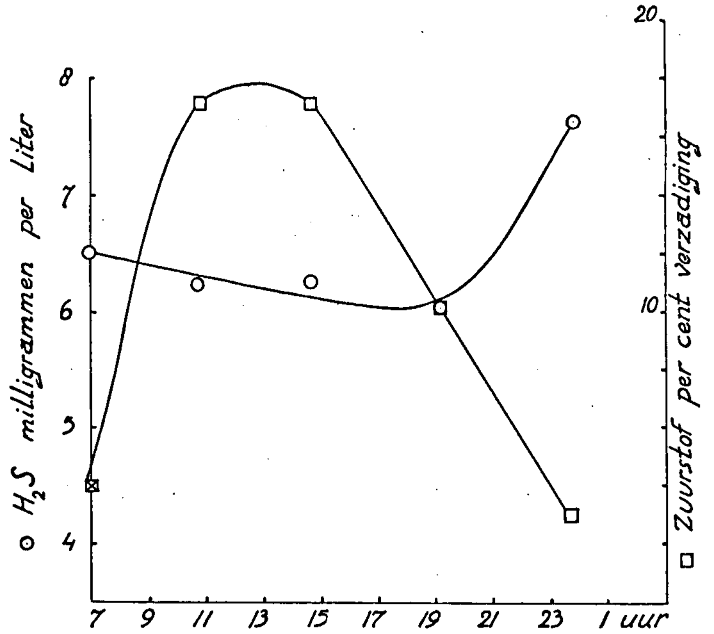


Figure IV.
H_2S and oxygen-content of the water during the day.

samples a known amount of standardized iodine solution and by titration of the excess of iodine with sodium thiosulphate. In August the amount of H_2S varied from 4.3—7.82 mg/L. As the samples for this examination were collected together with the samples for the oxygen determination the results could well be compared and the figure shows a minimum of H_2S when the amount of oxygen has reached its maximum whereas with decreasing amount of oxygen the H_2S increases and reaches its maximum after midnight.

So there was observed a striking correlation between the amounts of these two dissolved gases.

The third gas dissolved which was subject to our investigations was the carbon dioxide.

Carbon dioxide may be present in natural waters in three forms: free carbon dioxide or carbonic acid, bicarbonate and carbonate.

As the pH of the water of DF 7 proved to be 4, at this acidity the carbon dioxide occurs only in its free form; the amount of carbonate and of bicarbonate is so small as to be negligible.

This may be easily derived as follows:

$$k_1[H_2CO_3] = [H^+] \, . \, [HCO_3^-] \qquad (1)$$

$$k_1, \text{ the dissociation constant} = 3.5 \times 10^{-7}$$

The bicarbonate dissociates to carbonate:

$$k_2[HCO_3] = [H^+] \, . \, [CO_3^=]$$

$$k_2 = 4.7 \times 10^{-11}$$

As the concentration of hydrogen ions occurs in those equations, the influence of the pH on the ratio of the three forms of carbon dioxide will be of great importance.

When we take the total amount of carbon dioxide as 100, a third equation is:

$$[H_2CO_3] + [HCO_3^-] + [CO_3^=] = 100,$$

and combination with the other equations yields:

$$H_2CO_3 = \frac{100}{1 + \frac{k_1}{[H^+]} + \frac{k_1k_2}{[H^+]^2}}$$

In the water of DF 7 the pH is 4, so for the concentration of the hydrogen-ions we substitute $[H^+] = 10^{-4}$, which gives an amount of H_2CO_3 of 99.99 %.

It is quite clear that the amount of bicarbonate may be neglected.

The method given in the literature for the determination of free carbon dioxide is by titration with a solution of 1/44 N. sodium carbonate with phenol-phtalein as an indicator.

Considering the high acidity of the water of the peat bog it is improbable that this low pH is due only to the presence of carbon dioxide (see below).

With a solution of sodium carbonate we do not only determine the amounts of carbon dioxide but the sum of all acids present in the water. In consequence the results obtained by means of this method for the amount of carbon dioxide must be too high.

We tried to apply another method for the determination of the carbon dioxide. At first this method seemed unpracticable for field work but after some improvement it gave reliable results.

The principle is to lead an air-current, free from carbon dioxide, through the boiling water-sample into an Erlenmeyer-flask filled with barium hydroxide solution; the main current was divided into two smaller ones, one of which reached a flask with Ba-hydroxide directly, the other after passing through the boiling water sample.

Both Erlenmeyer-flasks contained the same amount of barium hydroxide and by titration with a standard solution of hydrochloric acid, the difference of the acid required gave a measure for the amount of carbon dioxide.

HÖLL (22) has investigated a great many peat bogs on their chemical composition; his data for carbon dioxide amount to 25 mg./L.; HÖLL states that in winter an amount of 30 mg./L. may be expected. HÖLL's data are obtained by titration with sodium carbonate.

Bij means of the new method the highest amount observed in DF 7 was 7 mg./L.

In the month of October the following data were observed:

TABLE IV.

Locality	Temperature of water	pH	mg./L. CO_2 new method	mg./L. CO_2 titration method.
Sphagnetum DF 7	9.6	4.0	6.7	15.0
Open water DF 7	9.6	4.1	6.4	7.6
„ „ „	7.8	4.0	5.76	9.75

In view of the data obtained we suspect that the data given in the literature for the amount of carbon dioxide in acid waters are probably too high. This is due to the method used and therefore a new method (in this case titration with barium hydroxide) should be preferred.

Quantitative changes in the three gases may be due to biological processes.

8. The acidity.

We had occasion to mention several times the high acidity of the high-moor peat bogs. To this acidity the peat owes its preserving qualities, as a great many bacterial processes are excluded in this range of pH.

Before discussing the possible causes of the low pH we will mention the observations made on the water of DF 7.

Determination of pH was carried out by means of the colorimetric method. To the buffers (SÖRENSEN and CLARK) were added indicators suited to the special range; addition of the same indicator (Brom-cresole-green or Brom-thymol-blue) to samples of the bog water and comparison of the coloured buffers allowed us to determine the pH of the water with an accuracy of 0.1.

The values of the pH were situated in the range from 3.7—4.1, the highest, 4.1, being observed in the open water of the bog directly after a rain storm; before the storm the pH was 4. This sudden increase of the pH demonstrates the fact that the bog water has no buffer-capacity.

The values for pH below 4 were observed in the Sphagnetum.

Observations during 24 hours showed no changes in the values for the pH except in one case, when the water of the Sphagnetum had a pH of 3.8 in day-time; the same night the pH had increased to 3.9.

A low pH could be expected from the literature. Several causes may contribute to explain this high acidity, the most plausible of which will be discussed here:

1. In the first place the amount of carbon dioxide is often considered as the important causal agens (HÖLL [22]).

This author apparently overestimated the capacity of this factor as shown by the following observations:

a. the bog water was boiled thoroughly in a hard-glass test tube; the increase of the pH did not exceed 0.2; in many cases no increase at all could be observed.

As we may expect that the whole amount of carbon dioxide is driven out by boiling the water, the gas does not seem to have much influence on the acidity of the water.

b. Due to photosynthesis the Sphagnetum should show considerable difference in pH during the day and night, if the acidity were chiefly caused by the carbon dioxide.

No such changes were observed by us, in accordance with MUENSTER-STRØM (31) who found that in the high-moor waters in Norway, where great quantities of green algae were actively assimilating, no increase in the pH could be observed.

c. The pH caused by a certain amount of carbon dioxide may be calculated very easily. According to JOHNSTON (23) carbonic acid, excess base [B+] and hydrogen-ion-concentration [H+], are related as follows:

$$[H_2CO_3] = \frac{\{[B^+] + [H^+]\}\,[H^+]^2 - k_w[H^+]}{k_1[H^+] + 2\,k_1k_2}$$

(k_w being the dissociation-product of water).

In case of the bog water $[B^+] = 0$ and substitution of H_2CO_3 yields $[H^+]$ and, accordingly, pH.

Substituting the maximal amount observed in DF 7 (6.7 mg./L.) a pH of 5.3 should be the result, whereas the maximal amount given by HÖLL (30 mg./L. CO_2) yields a pH of 4.8.

In both cases the pH is far too high, considering the actual value of about 4.0.

The conclusion seems, therefore, warranted that in the insufficiently buffered milieu the carbon dioxide will cause a certain decrease of the pH, but in no case the low pH should be attributed exclusively (or even for an important part) to the presence of carbon dioxide.

2. The same consideration holds for the influence of sulphuretted hydrogen upon the pH; the amounts present in the bog water may only cause a change in the second decimal place of the pH.

3. Nor can much value be attached to the opinion of SKADOVSKY (42) that ferro- and aluminum salts cause a pH < 4 in Russian high-moor bogs. As the analysis of the water of DF 6 gives an amount of ferro-ions less than 0.1 mg./L. no such influence may be expected.

4. The presence of small amounts of organic acids in the water of bogs seems a well established fact.

As the results of the microbiological survey showed the presence of butyric-acid bacteria, it is quite probable that butyric acid and other organic acids are present in the water.

The method of DUCLAUX (12) was used in the laboratory to investigate the presence and quantity of volatile organic acids. By distillation and fractional titration of the distillate the presence of small and varying quantities of butyric or valeric acids could be demonstrated.

Those acids also contribute to a decrease of the pH but neither of the above mentioned acids may be considered as the main factor in the problem of the acidity, as the amounts were much too small.

Three more important theories remain to be discussed:

5. ODÉN (34, 35) and his school attribute the acidity of bog water to the influence of humic acids,

6. PAUL (36) to an active secretion of an unknown acid by the cell walls of the Sphagnum,

7. BAUMANN and GULLY (4) have propagated the idea that humus and the cell walls of Sphagnum are able to exchange ions with the environment so that hydrogen-ions are set free by absorption of the kation.

This latter theory, which preceded that of ODÉN, has met with much opposition, but the observations made on the mineral environment of the peat bog have impressed us with its plausibility so that we prefer it to both PAUL's or ODÉN's speculations.

The observations on the humic acids carried out by ODÉN and his collaborators lead to a division of the humic acids in three groups; one of them, the "fulvic-acid" group, constitutes the soluble substance, and, according to ODÉN, the cause of the brownish-yellow colour of the water in peat bogs is due to fulvic acids. No further observations have been made about the composition and chemical properties of the fulvic acids.

The water of DF 7 had a yellow colour, but could be made colourless by filtration through a Seitz filter; as the pH did not change after the filtration there seems to be no correlation between the yellow colour (eventually caused by fulvic acids) and the pH.

The other humic acids are considered by ODÉN as to be tetrabasic acids. By measurement of the conductivity ODÉN concludes that they are able to cause a low pH when dissolved.

WEHRLE (53) attributes a great importance to the presence of humic acids in the bog waters of high-moors, but HÖLL has opposed this statement of WEHRLE by referring to a great many peat bogs with a low pH and apparently, without humic acids.

Considering those observations and the uncertainty of the composition of those acids, the chief cause of the high acidity cannot be attributed to a direct influence of those acids. Their possible indirect influence will be treated under the discussion of the theory of ionic exchange.

PAUL's observations on the "Kalkfeindlichkeit" of Sphagnum have lead him to believe that the Sphagnum plants secrete an acid; in an alkaline milieu the acid is immediately neutralized and the plant proceeds to produce more acid, by which overproduction it exhausts itself. The concentration of the alkali has no importance but the total amount seems to dictate the process.

The observations of PAUL have stimulated many investigators to study the problem. By their results it is shown that the different species of Sphagnum show a different reaction on the substrate and on the pH of the environment.

The main interest of the later literature on this subject seems to be in the direction of the influence of the substrate on the Sphagnum plant, whereas the influence of Sphagnum on the environment has been neglected.

BAUMANN and GULLY consider the cell-wall to be a colloid which, when placed in a salt-solution, absorbs the kations exclusively and sets free the acid.

Much opposition to the theory of BAUMANN and GULLY, headed by ODÉN and his school, resulted in the abandonment of the exchange-theory during many years, until FREUNDLICH (15) pointed out its importance for colloid chemistry. Zeoliths and aluminum silicates brought in contact with neutral salts cause a decrease in the pH of the salt solution and FREUNDLICH claims a similar behaviour for the cell walls of Sphagnum, based upon the observations of BAUMANN and GULLY.

This so-called "Neutralsalzzersetzung" has since long been subject of many investigations in Soil Science. The experimental fact on which it was originally based is: that an extract of humus-soil in a neutral salt solution (as for instance potassium chloride) shows a higher acidity than an extract of the same soil in pure water.

TRÉNEL and HARADA (48) have given a discussion of the current literature on this subject.

As to the influence of the Sphagnum plants on the acidity of the substrate we mention the observations of SKENE (43) who obtained a marked decrease of the pH by growing Sphagnum in a solution of sodium chloride.

Further observations were made by STELMACH (44) on the conduct of *Sphagnum recurvum* and *Sphagnum cymbifolium* in solutions of different initial pH. Both species of Sphagnum are able to reduce the pH when grown in a weakly alkaline solution; *Sphagnum recurvum* causes an increase of the pH when the initial pH is too low for its development, whereas *Sphagnum cymbifolium* perishes under these conditions.

Those different theories and experiments are fully discussed here because our observations made on the pH and the mineral environment of DF 7 might be explained by accepting an exchange of the kations of the available chlorides with hydrogen-ions from the Sphagnum cell walls or from the humus of the soil (the above-mentioned, indirect, influence of humus!), which process leads to the formation of free hydrochloric acid.

The amount of chlorine ions determined in DF 7 (when supposed to be present as hydrochloric acid) gives a pH of 3.8.

The field observations were followed by experiments, partly carried out by Dr. W. BEIJERINCK at the Biological Station at Wijster, partly by some of us in the Botanical Institute at Leyden.

The experiments of BEIJERINCK had a preliminary character: plants of *Sphagnum cuspidatum* Ehrh., fa. *plumosum* Paul (a submerse species) and of *Sphagnum magellanicum* Bridel, var. versicolor Warnst. (an emergent species) were brought in flasks containing rain water. Three different series were observed:

a. with living Sphagnum
b. with dead Sphagnum
c. with a recent peat.

A fourth flask, containing rain-water, served as a control.

At regular intervals the pH was determined in the 4 flasks by means of the colorimetric method. The results are shown in the following table:

TABLE V.

	Sphagnum cuspidatum				*Sphagnum magellanicum*			
pH of	living	dead	peat	control	living	dead	peat	control
after 5 min. ...	5.1	5.1	5.1	5.1	5.1	4.8	4.6	5.1
„ 1 hour ...	5.1	4.8	4.8	5.1	5.1	4.2	4.6	5.1
„ 5 hours...	5.0	4.6	4.5	5.1	4.4	4.2	4.3	5.1
„ 7 „ ...	5.0	4.6	4.5	5.1	4.4	4.2	4.3	5.1
„ 22 „ ...	5.0	4.5	4.4	5.1	4.2	4.2	4.2	5.1
„ 24 „ ...	5.0	4.5	4.4	5.1	4.2	4.2	4.2	5.1
„ 2 × 24 h.	5.0	—	—	—	4.1	4.1	4.1	5.1
„ 3 and 4 × 24 hours no more change.								

Another series of, more exact, experiments were undertaken:

Equal volumes of water-soaked *Sphagnum cuspidatum* and *Sphagnum cymbifolium* were submersed in equal volumes of rain water, which had been standing during 24 hours in Erlenmeyer-flasks of Jena-glass in which time the pH did not change.

Table VI shows the results of these experiments:

TABLE VI.

	Sphagnum cuspidatum		*Sph. magellanicum*		control
	pH of living	dead	living	dead	water
after ½ hour	5.3	5.0	5.0	4.8	5.3
„ 3 „	5.2	4.6	4.4	4.3	5.3
„ 6 „	5.1	4.5	4.4	4.3	5.3
„ 24 „	5.1	4.5	4.4	4.3	5.3

„ 2 and 3 × 24 hours no further changes were observed.

The experiments of BEIJERINCK show the influence exerted by the Sphagnum plant on its environment. Whether this influence (the decrease of the pH) is due to the secretion of acids or to an exchange of ions does not appear from these observations.

Further experiments were carried out by Mr. K. VAAS.

A culture of *Sphagnum cymbiolifum* was used. The plants were placed in Erlenmeyer-flasks of quartz in twice distilled water; we may expect no measurable ion-exchange between the quartz and the water. Thus, if the Sphagnum secretes an acid the pH of the distilled water should show a decrease. On the contrary, a slight increase was observed after the lapse of two days, probably due to the changes in the carbon dioxide tension as influenced by photosynthesis and respiration.

By this experiment evidence was obtained that the Sphagnum plants do not produce acids in the medium in which they grow.

Other experiments were carried out by placing the Sphagnum plants in a very diluted solution of ammonium chloride in quartz or paraffined glass. The composition of the initial solution was exactly determined as well as its pH. During a few days the plants remained in the solution, after which the composition and the pH were reexamined.

Without any exception the amount of ammonium-ions had decreased, whereas no change could be observed in the amount of chloride-ions.

The pH often decreased but there seemed to be no definite correlation between this decrease and the amount of NH_4^+ absorbed by the plants. The uncertainty of these results is in part due to the relative precision in the method of the NH_4^+ — and Cl^- determination. The latter determination is inexact when compared with the NH_4-determination, which was carried out spectrocolorimetrically. It seems therefore possible that small amounts of chloride or chloride-ion were also absorbed by the moss. Neither were influences of photosynthesis and respiration excluded. It seems more promising to carry out future investigations with dead Sphagnum, inasmuch as this material seems equally capable of ionic-exchange. As these investigations would be non-biological, we shall have to rely in the future upon the results of colloid-chemists.

The possibility mentioned by FREUNDLICH, according to which the exchanged kation does not need to be hydrogen but may very well be a metal, also has to be investigated and might have obscured the results of our experiments.

At present the exchange-theory seems the only one, however, which may account for the observed facts.

9. Temperature of air and water.

A maximum and minimum thermometer were placed in a distance of 15 cm. from the bottom in the Caricetum. The temperatures shown by this thermometer differed 1—2° C. from the temperature observed by the meteorological substation at Wyster. This difference may be due to the higher position of the latter thermometer which was placed at a height of 2.25 m. During 24 hours the temperature varied from 15.3° C.—22.0° C.

The water-temperature showed a marked lag in relation to the air temperature and the fluctuations are damped as compared to the air temperature. The bottom of the pond was always colder. Inverse stratification did not occur.

Humidity.

The humidity-data of the environment were obtained by means of a psychrometer of a very simple construction: the different temperatures of a dry-bulb and a wet-bulb thermometer were used as a measure for the humidity of the air. The "Carrier Engineering Corporation's Psychrometric Chart" mentioned by SHELFORD (41), gives the correlation between temperature of wet and dry bulb and percentage of relative humidity. The relative humidity varied from 70—97 %. The influence of a rainstorm was shown by a sudden increase from 92 % tot 95 % of relative humidity in the afternoon of August 30th.

The evaporimeters used for the measurement of the evaporation in different layers were constructed of the type of the porous cup atmometer. On the top of a calibrated tube was placed a cup with porous walls; a cotton wick reached from the cup into the water. Evaporation was determined by measuring the loss of water in the calibrated tube. As the instrument had not been standardized, only relative observations resulted from this method.

The atmometers were placed on different levels in the Sphagnetum: 0, 5, 10 and 15 cm. from the bottom. The observations showed a larger amount of evaporation at the bottom — in the Sphagnetum — than was found in the higher layers. Those observations lead us to the view that possibly the Sphagnum should be able to diminish the humidity of the atmosphere by an intensive absorbtion of the atmospheric water.

The following experiments were carried out at the Laboratory at Leyden by Miss A. KRIJTHE and Mr. H. VERDAM to investigate the absorbtive capacity of Sphagnum.

Plants of *Sphagnum cymbifolium* were dried in a desiccator over sulphuric acid during two days. Aliquots of this dried Sphagnum were brought under a bell-jar in which was placed a solution of sodium chloride of a known molarity. The material was placed on the scale of a balance and fixed to the beam by means of a paraffined thread which passed through the wall of the bell-jar.

The amount of the water absorbed by the Sphagnum could be determined in this way.

Immersed in water the dried Sphagnum absorbed 10 × its weight.

TABLE VII.

In the bell-jar above water-rel. humidity 100 % Sph.-absorbs ± 2 × its weight.

In the bell-jar above 1 mol. NaCl rel. humidity 96.4 % Sph.-absorbs ± 1 × its weight.

In the bell-jar above 2 mol. NaCl rel. humidity 91.25% Sph.-absorbs ± 1/2 × its weight.

In the bell-jar above 3 mol. NaCl rel. humidity 86.6 % Sph.-absorbs ± 1/3 × its weight.

In the bell-jar above 4 mol. NaCl rel. humidity 79.5 % Sph.-absorbs ± 1/4 × its weight.

In the bell-jar above 5 mol. NaCl rel. humidity 69.2 % Sph.-absorbs ± 1/5 × its weight.

The relation between relative humidity of the air and amount of water absorbed by Sphagnum is clearly shown by the experiments.

10. Pollen-analysis.

At point III, the S—W corner, a hole was dug and samples were taken from every 10 cm down to 60 cm, where the hard sand was encountered. The samples were studied by Miss A. KRIJTHE in the usual way and the relative frequency of the various pollens was

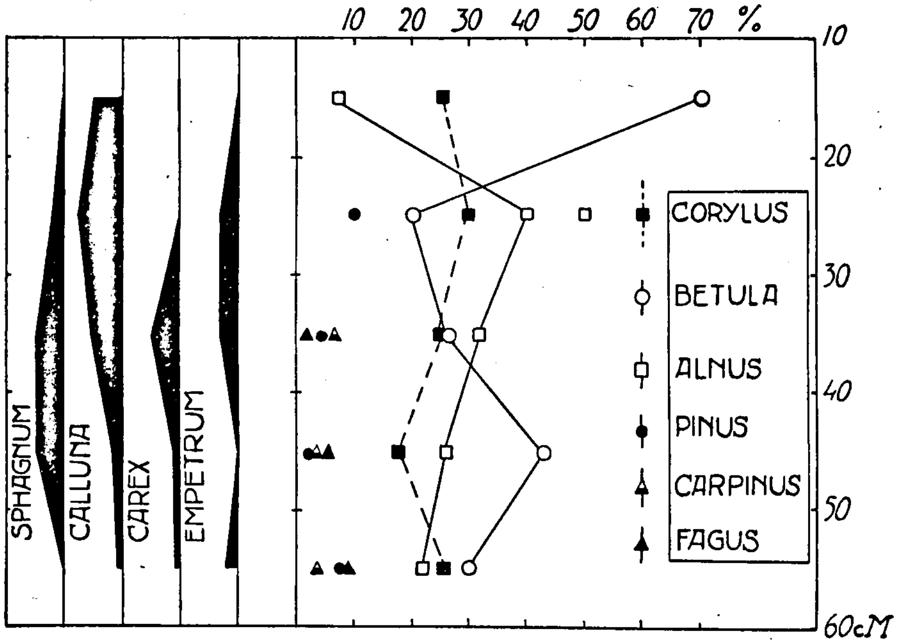


Figure V.
Pollen-diagram from D. F. 7.

established (average of three counts). The % is given of total tree-pollen (genera marked *).

Figure V shows the conventional pollen-diagram as a function of depth. It appears that the only other significant difference from this diagram with other samples from Drenthe (see FLORSCHÜTZ c. s. [14]) is the preponderance of birch-pollen, although the small number of grains found near the surface and near the bank make the percentage-data very uncertain. On the whole, the diagram is characteristic of a young peat of the sub-atlantic to subboreal type. A "pollen archive" of recent plants proved to be very useful. By means of this collection

TABLE VIII.

Genera \ Depth	10–20 cM. roots and sand		20–30 peat and sand		30–40 dry peat		40–50 wet peat		50–60 sandy peat	
	freq.	°/₀	freq.	°/₀	freq.	°/₀	freq.	°/₀	freq.	°/₀
*Betula.	3	70	2	20	33	26	132	43	14	30
*Alnus		6	4	40	42	32	77	26	10	22
*Tilia.					2	2	5	2	1	2
*Fagus					2	2	10	4	4	8
*Quercus. . . .					2	2	5	2		
*Corylus	1	24	3	30	32	25	49	17	12	26
Myrica					3		39		8	
Sarothamnus.	2		2		5		19		3	
*Salix						1				
*Pinus			1	10	14	3	5	2	4	8
Sphagnum . .	5		12		57		55		4	
Carex	2		1		52		18		12	
Calluna	10		15		11		3		3	
Erica			5		4		5		1	
Empetrum . .									1	
Andromeda .	2		2				1			
Vaccinium . .			4				1		1	
Genista					1		12		1	
Melampyrum							1			
Euphrasia . .					3		10			
Gentiana . . .							4			
Campanula. .							5			
Drosera									1	
Eriophorum .			1		2				1	
Polypodium .							2			
Lycopodium?										
*Carpinus. . .					9	7	10	4	2	4
	25.5		52.25		265		468		83.75	

a fair picture could be obtained of the flora of the strata 30—40 and 40—50 cm respectively.

In the former stratum *Carex, Eriophorum* and *Calluna* occur abundantly, while *Myrica, Genista, Euphrasia* and *Campanula* are more frequent in the deeper layer, where *Calluna* is less frequent. In both cases the dominant trees are birch and alder. The frequency of some plants is given in Table VII together with the tree-pollen.

It may be that the "bank", which forms the lower boundary of the peat, corresponds to the sandy bottom of the pool, and that another layer of plant remains may occur below this stratum.

From this survey it seems, however, that the peat of D. F. 7 is of comparatively recent origin; there appears to be no reason to date it earlier than the subboreal.

The Life-Cycle in a Sphagnum-Bog.

From our field and laboratory experience, scanty as it is, supplemented by a study of the literature, a concept of the life-cycle in a Sphagnum-bog may be derived.

Oligotrophic by the low mineral contents, dystrophic by its high acidity, the waters of the bog represent a very special condition, which condition constitutes a specific milieu. The vital counterpart of this milieu gives us the life-cycle, which is dominated by the poverty in electrolyte and in oxygen and by the extremely high acidity.

D. F. 7 apparently is partly ombrogenic, partly soligenic in nature. The rain water which feeds it, contains Calcium, Magnesium, Sodium, Potassium and Ammonia; sulfate, chloride, nitrate, carbon-dioxide, Nitrogen and Oxygen. The kation will be partly exchanged by the Sphagnum for hydrogen-ions, thus causing the high acidity. The sulfate will be reduced to sulphide which, at the low pH, will form H_2S. The oxygen production by photosynthesis is not able to oxidize all of the H_2S. Aerobically, the H_2S may be oxidized to $SO_4^{=}$ again by autotrophonts. Nitrate, if present, will be reduced to nitrogen, while nitrification seems to be inhibited. Due to the presence of butyric acid bacteria, anaerobic fixation of nitrogen does not seem to be excluded.

The formation of methane was demonstrated in the field; anaerobic decarboxylation of lower fatty acids may be its cause. Oxidation of methane and hydrogen is possible, but was not established. Decrease of pH due to the photosynthetic intake of carbon dioxide was only observed in laboratory experiments. In the field the CO_2 contributes but little to the actual acidity of the bog. The same is true for the organic acids, which occur, moreover, in variable amounts. The presence of valeric- and probably of butyric acid could be demonstrated.

Anaerobic decomposition of cellulose seems very slow; the lignin (or perhaps the ligno-protein) complexes are decomposed but the bacterial components in this process are imperfectly known, despite

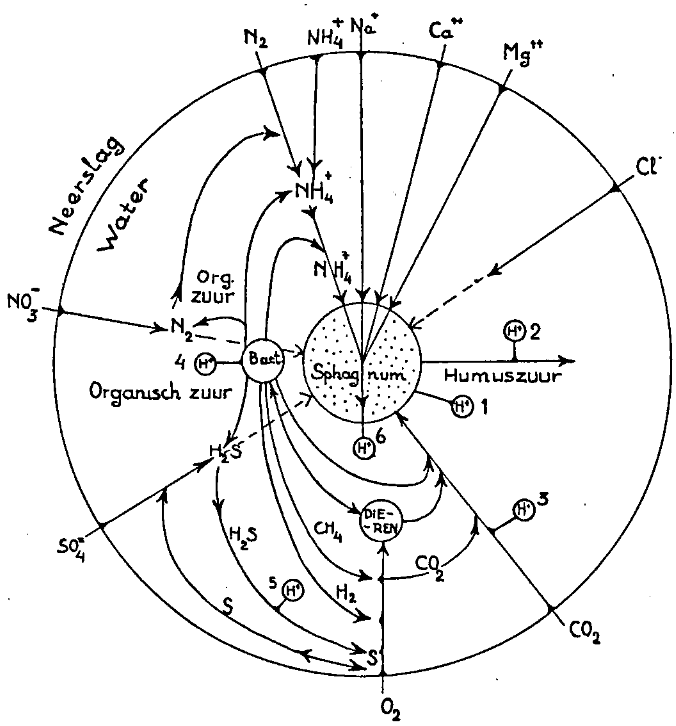


Figure VI.

Life-cycle in a Sphagnum bog.
org. zuur: organic acid.
neerslag: precipitation.
humus zuur: humic acid.
dieren: animals.

the beautiful work of WAKSMAN (52). In view of the work of K. GRIFFIOEN (19) who demonstrated the formation of humic acids from lignins in the heart-wood of Ebony under presumably sterile conditions, it seems possible that many of these reactions might ultimately prove to be non-vital. Figure VI shows a diagrammatical representation of the life-cycle in the bog.

The circumference of the circle represents the boundary of atmosphere and water. From the atmosphere the bog receives Ca^{++}, Mg^{++}, Na^{+}, NH_4^{+}, N_2, NO_3^{-}, $SO_4^{=}$, O_2, CO_2 and Cl^{-}. The processes described above are described by lines and arrows in the figure; the Sphagnum is placed in the centre. From the above it also appears that the chloride-ion, while taken up by the Sphagnum (as may be shown by the ash-analysis) still remains as the biologically-stable component in the water. Due to its preponderance it will act as chief partner for the exchanged hydrogen ions, so that we are driven to the conclusion, mentioned before in this paper, that the reaction of the bog water is chiefly due to hydrochloric acid. As the water is unbuffered, a single rain-storm is sufficient to raise the pH! Presence of buffer (unless it be situated near the equilibrium-pH) might cause the death of the Sphagnum, in accordance with the observations of STELMACH (44) and SKENE (43). Photosynthesis seems most active in the emerged parts of the moss. The conduction of water (according to experiments by Dr W. BEIJERINCK) seems to be downward, which seems to be in harmony with the findings of Miss BOWEN (9) for other mosses. While Sphagnum seems able to absorb moisture from the atmosfere, the amount taken up by this process seems hardly sufficient to saturate it fully with water.

A capillary film of liquid water has to be present at its exterior. Indications of a "vapour layer" from 5—10 cm above the bog could be obtained from atmometer-observations, although a definite proof is lacking. During the short period of our observations, no significant differences could be observed between water and air temperatures, although on top of the Sphagnum "cushions" very high temperatures have been recorded.

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