AN ECOLOGICAL STUDY OF AQUATIC HABITATS IN NORTH-WEST OVERIJSSEL, THE NETHERLANDS

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SUMMARY

During summer 1967 an ecological study of the zonation of different macrophytes was made in the three basins of Chielgat, Venematen and Zuideindigerwiede in North-West Overijssel, the Netherlands. Chemical properties of sapropels, microclimatic conditions and composition of mud gases in habitats of different macrophyte zones were studied.

The three basins show various degrees of trophism and different qualities of humic substances in sapropels. The habitats of different macrophytes in the same basin are also different.

Each vegetation zone is characterized by a special temperature course in different water and air layers. The temperature course is dependent on the position and structure of the vegetation zone and on weather conditions. Water temperature is influenced by the duration of insolation, and by the direction and strength of wind. Time-shifts in the warming-up of the lower water layers are also of interest.

The relative amounts of CO_2, O_2, N_2 and CH_4 were estimated both under and in the plant cover of the vegetation zones under study. While under the plant cover CH_4 prevails in the gas mixture, in the plant cover CO_2, O_2 and N_2 are of higher importance. The amount of $CO_2 + CH_4$ on the one hand and the amount of N_2 on the other hand reflect the outputs of C and N metabolisms which take place in the basins. The gaseous output of C and N metabolisms in the basins under study are related to the trophisms of individual basins.

1. INTRODUCTION

The present report is based on the results obtained from an ecological study of aquatic habitats supported by the Dutch organization for Pure Research (Z.W.O.), The Hague, the Netherlands.

The methods employed were aimed at obtaining analytical data concerning the catabolic part of the total turn-over of organic material in the aquatic ecosystem.

Studies of ecological relations in aquatic biological communities have a long tradition in the Netherlands. This is evident from a great number of papers published on the subject in the last decades (Westhoff 1951, Westhoff & Van der Voo 1961, Westhoff 1964, Kuiper 1958, Van Donselaar 1961, Segal 1966a, b, Segal & Groenhart 1967, Segal 1968). Research in this field is chiefly directed to the influence of water depth, pH, currents, wave dash, etc. on various macroaquatics and on aquatic plant communities.

During the summer of the year 1967, the present author studied certain environmental factors (metabolism in sapropels, microclimatic conditions and properties of the substrate) in *Stratiotes aloides* vegetations and in the adjacent vegetational zones of several basins in the lake district of North-West Overijssel, the Netherlands. The investigations were carried out along different lines which are thematically related but methodologically divergent.

The biological and chemical characteristics of sapropels, linking the anabolic and the catabolic processes of the turn-over of aquatic ecosystems, are of primary importance and had been studied by several authors (*cf.* GJESSING 1967, POVOLEDO 1967, SHAPIRO 1957, 1967). Sapropels represent the final product of the decomposition and humification of organic matter in water basins and, at the same time, provide a nutritive and physically supporting substrate for macrophytes. The properties of a sapropel often assist the invasion of the site by certain species and may exert decisive influence on their subsequent settlement or extinction. The important effect of humic substances on the germination of plant diaspores has, for instance, been documented by a number of papers (cf. FLAIG 1968).

The present author studied the chemical characteristics of samples of sapropelic deposits in three lakes. The samples were collected in transects from the open water through the successive zones of aquatic vegetation to the shore.

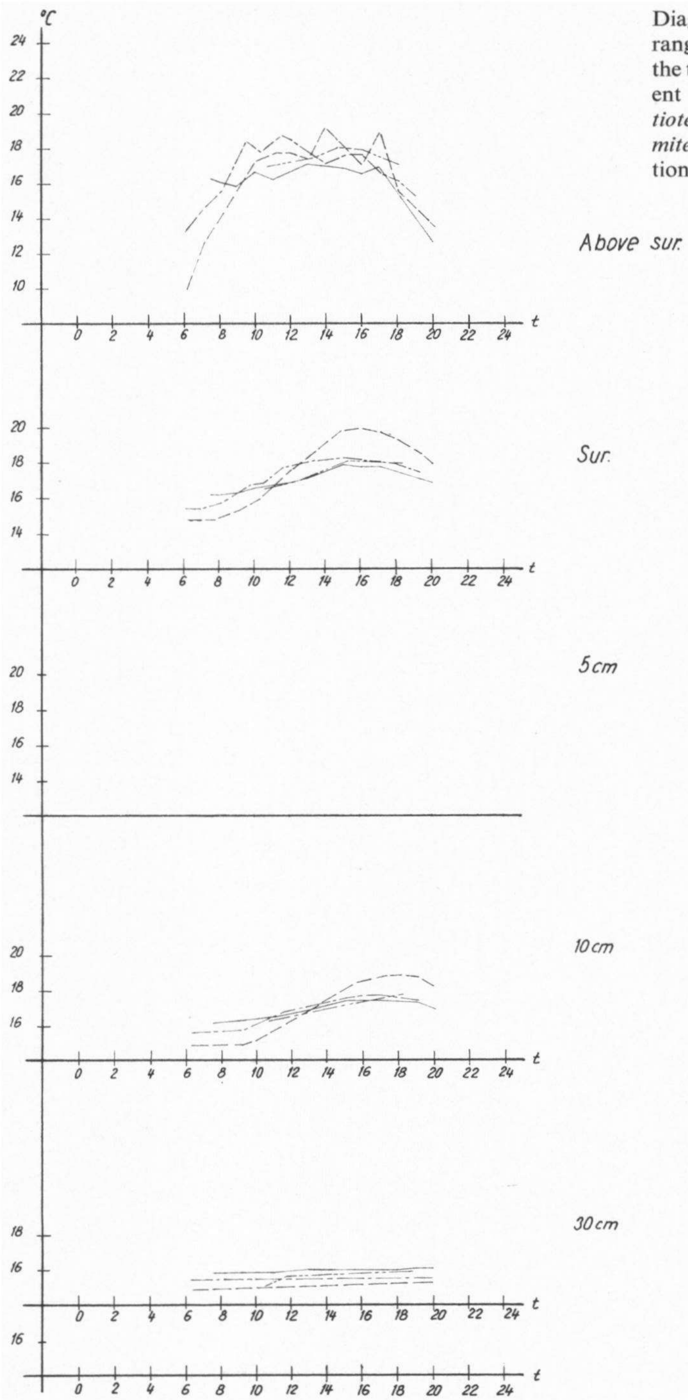
During completely aerobic decompostion of organic matter in a sapropel only CO_2 is released. At lower tensions of oxygen, under semi-anaerobic to anaerobic conditions, the decomposition of such substances as cellulose, hemicelluloses, proteins, organic acids and alcohols results in the production of methane (CH_4). Depending on the degree of anaerobiosis, the quantities of CH_4 produced in this way may equal or even exceed those of the released CO_2. The production of methane as a by-product of anaerobic metabolic processes is brought about by the activities of the highly specialized physiological group of bacteria living in flooded soils, in water-logged sediments, such as peats and oozes (both in fresh water environment and in the sea), and also in the digestive tract of higher vertebrates. BARKER (1941) found this group of bacteria to be highly heterogeneous as far as their morphology is concerned, but nevertheless classified them all as belonging to the same family, that of *Methanobacteriaceae*.

The methane produced by the biological breakdown of organic matter can be re-metabolized by microorganisms of a type classified by LEADBETTER & FOSTER (1958) in the genus *Methanomonas*. During this aerobic biological oxidation of CH_4, O_2 is consumed and CO_2 is produced. The relative amounts of CO_2, CH_4, O_2, H_2 and N_2 in the rhizosphere of aquatic vegetation characterize the degree of aerobiosis or anaerobiosis in a particular habitat, CO_2 and CH_4 representing the ultimate metabolic products of the carbon cycle; and gaseous N_2, that of the nitrogen cycle.

During the present investigation, gas chromatography was employed to study relative quantities of the above-mentioned gases in the rhizosphere, in water, and in the vegetation of macrophytes.

2. MATERIAL AND METHODS

The field work was carried out in three lakes with different degrees of trophism:



Diagr. 1. Examples of range and fluctuation of the temperature on different days in mixed *Stratiotes aloides* and *Phragmites communis* vegetation in the Chielgat basin.

the Chielgat near Oldemarkt, the Venematen near Vollenhove, and the Zuideindigerwiede near Wanneperveen. Field observations and measurements of microclimatic conditions were carried out from floating bridges specially constructed for the purpose and giving access to the successive zones of aquatic vegetation. The following vegetational zones were studied in the Chielgat: the *Ceratophyllum demersum* zone, the *Utricularia vulgaris* zone, the zone of submerged *Stratiotes aloides*, the zone of emerged *Stratiotes*, and the zone with *Stratiotes* and *Phragmites*. In the Venematen basin, vegetation with *Stratiotes aloides* and *Cicuta virosa* was studied; and in the Zuideindigerwiede, that with *Stratiotes aloides*, *Utricularia vulgaris*, and *Cicuta virosa*.

The sampling of the sapropelic deposits for chemical analyses was performed from floating bridges or from a motor cruiser. A special 2 m long sampling tube was used; it was provided with a ladle to collect the samples. The ladle could be closed under water by means of a sliding valve operated from the bridge or boat.

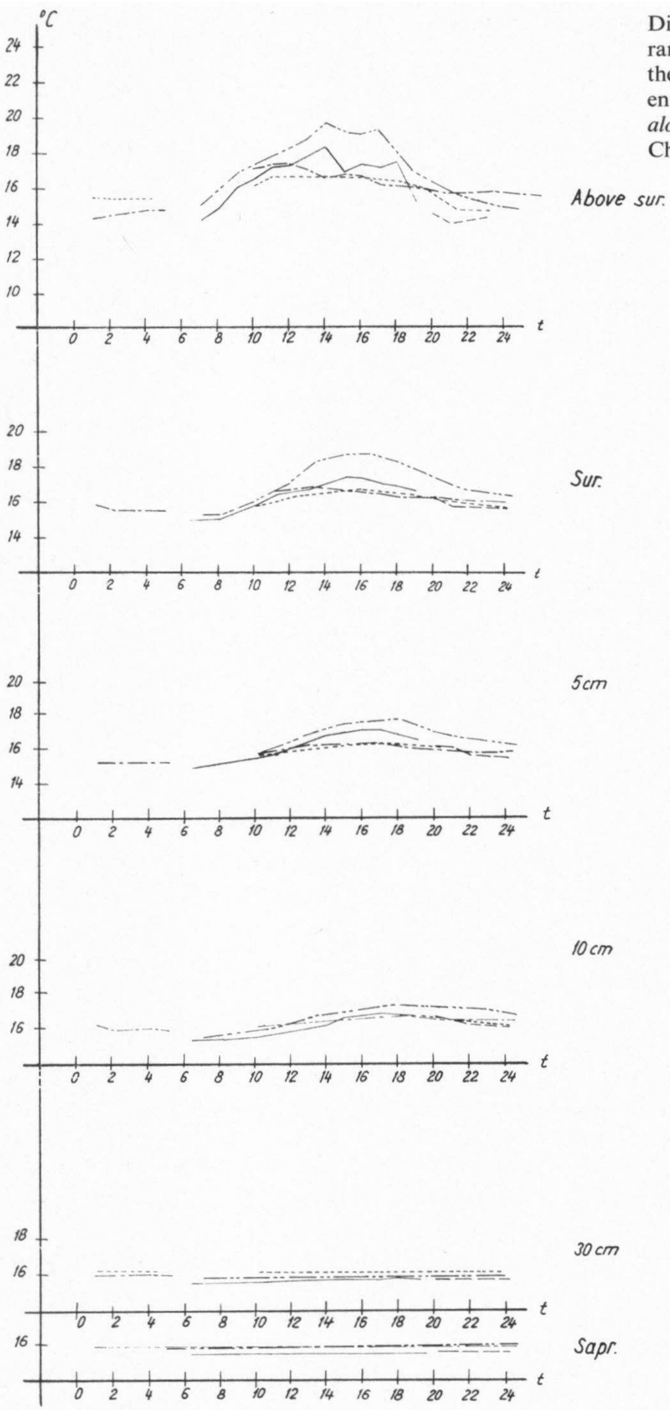
The dry-matter content of the sapropel samples was determined gravimetrically after desiccation to constant weight at 105 °C. The total amount of organic matter in sapropels and in fractions of sapropel samples was estimated by titration after total oxidative destruction with potassium bichromate according to SPRINGER & KLEE (see THUN, HERRMANN, KNICKMANN 1955, p. 49). Total N-content in sapropel and in humus fractions was determined by means of a modified Kjeldahl method (JACKSON 1958, p. 183). Exchangeable ions in sapropels were determined complexometrically (according to MORAVEC 1960). Humus fractions were determined by means of the method developed by SPRINGER & HOOK (see THUN *et al.* 1955), as modified by AMBROŽ (1960). Temperatures were read in selected vegetation zones from the floating bridges both directly by installing thermometers at various depths, and electrometrically by means of thermocouples and thermistors connected to Withoff or Electrofact automatic recorders. Temperatures were taken during stretches of 3 to 4 days each at the following depths according to the local vegetational structure:

1. air temperature above the water,
2. just below the water surface (depth almost 0),

3–5. at depths of 5, 10, and 30 cm below the water surface,

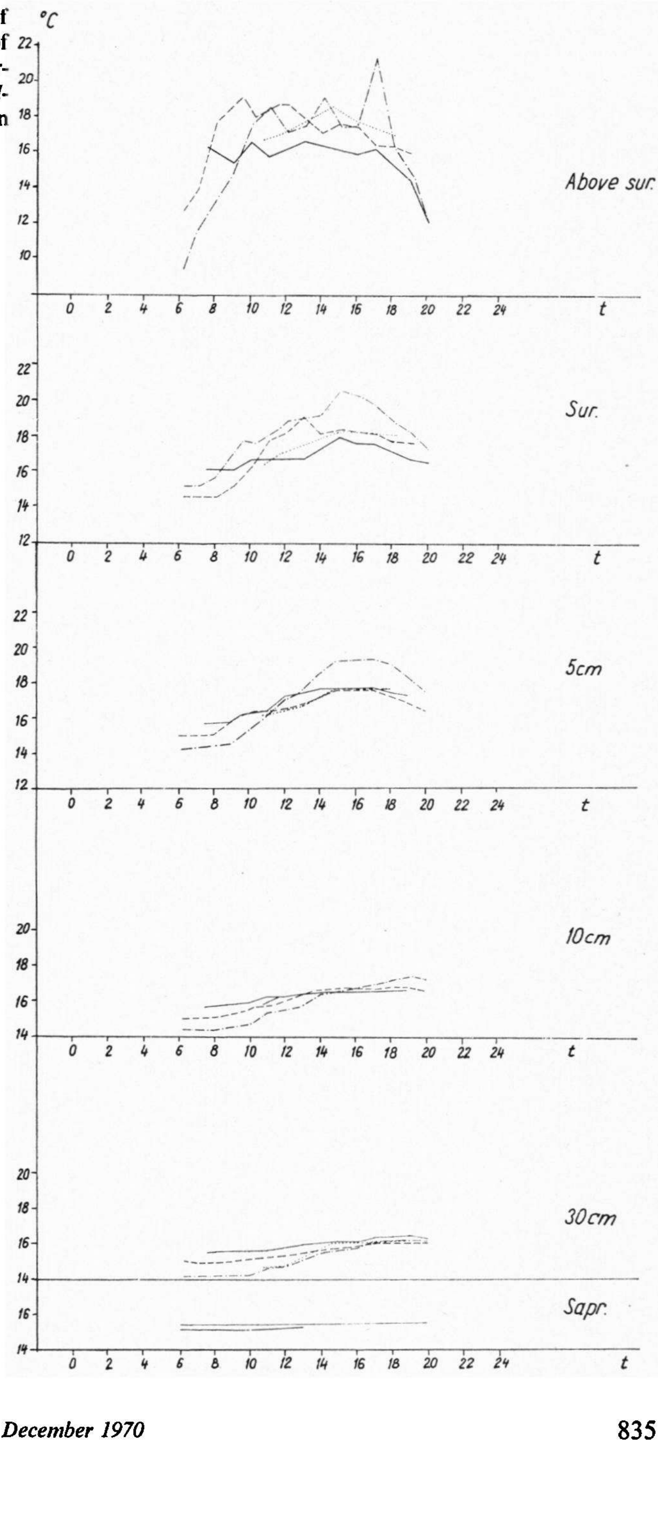
6. in the sapropelic deposit.

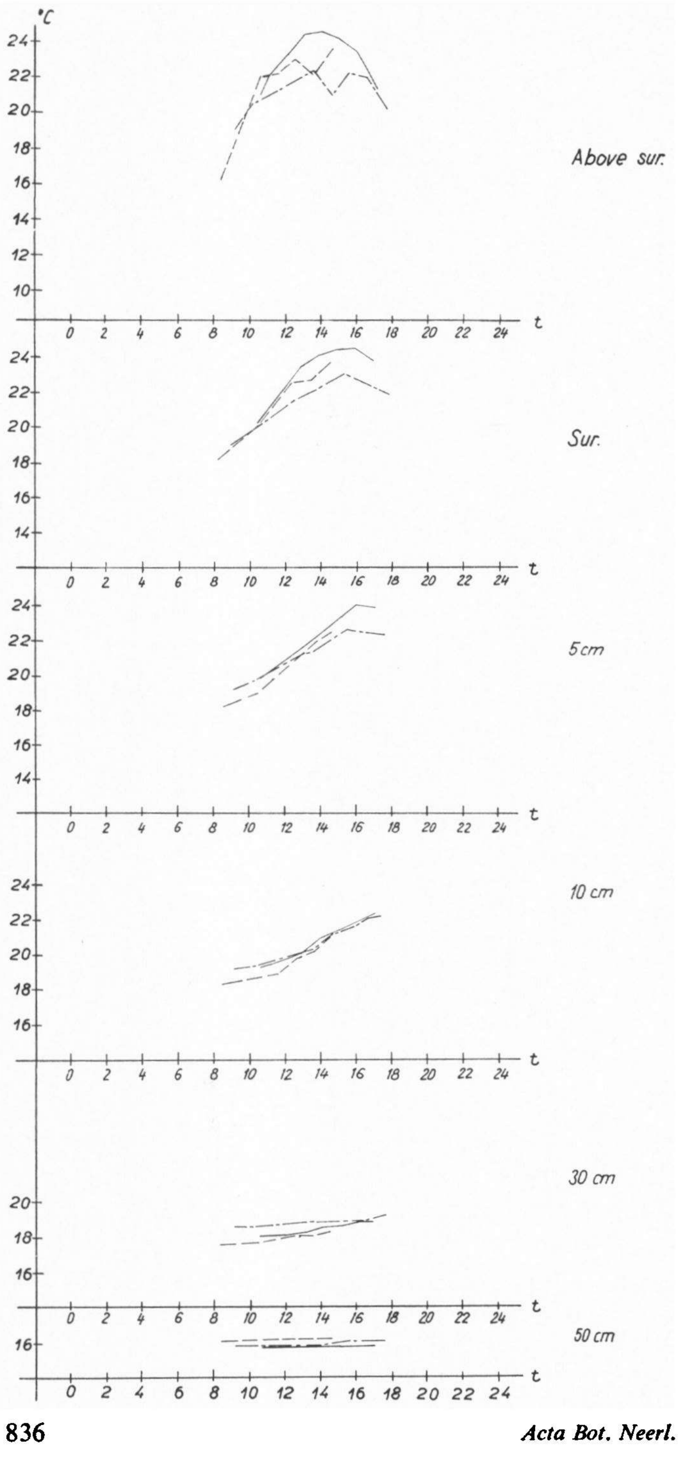
The composition of the mud gases was studied in preselected vegetational zones both in the sapropelic bottom layer and in the vegetational stand. Gas samples were collected in the following way: to a funnel tube a piece of rubber tubing was attached and this, in turn, was fastened to a test tube. The whole system was filled with water. By inverting the funnel the gaseous fraction accumulated in the test tube. As soon as a sufficient quantity had assembled, the test tube was closed under water with a special rubber stopper and taken to the laboratory for analysis in a home-made gas analyser (Ústav instrumentálni analytické chemie ČSAV Brno). Hydrogen and argon were used as carrier gases, the pressure to produce the flow being kept at about 0.25 atm. The apparatus for gas chromatography had two columns: one filled with Si-gel, and



Diagr. 2. Examples of range and fluctuation of the temperature on different days in *Stratiotes aloides* vegetation in the Chielgat basin.

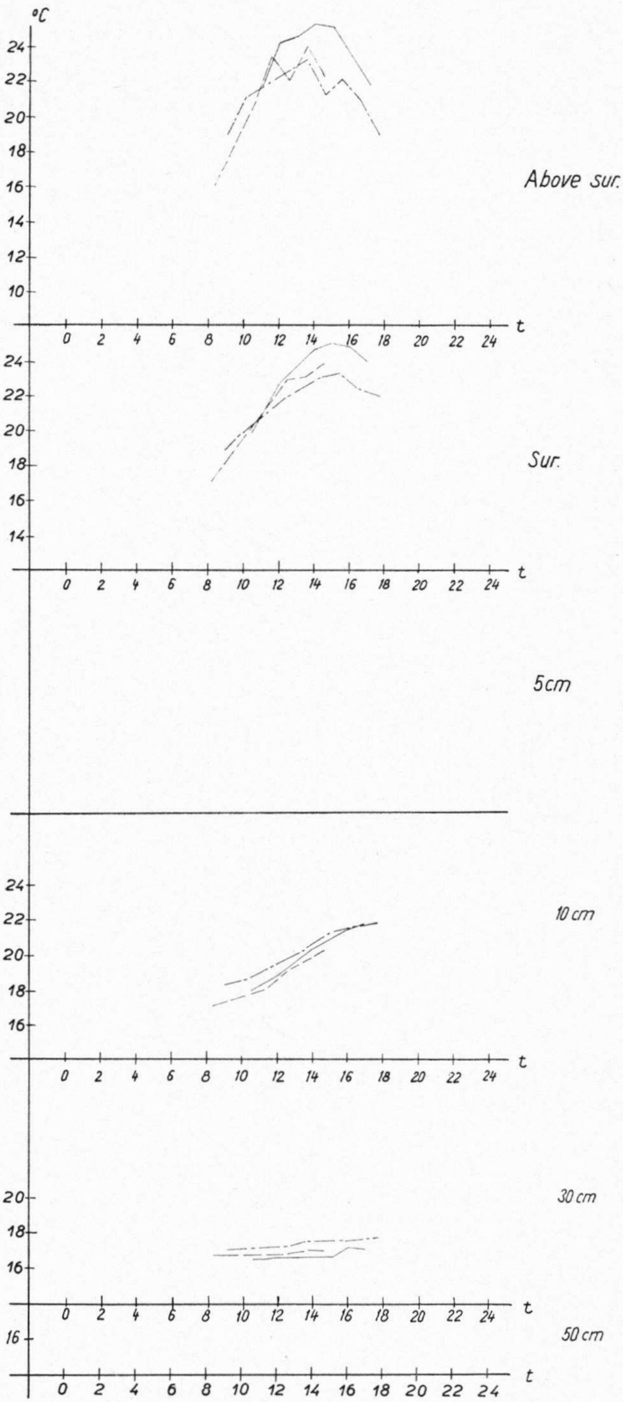
Diagr. 3. Examples of range and fluctuation of the temperature on different days in *Ceratophyllum demersum* vegetation in the Chielgat basin.

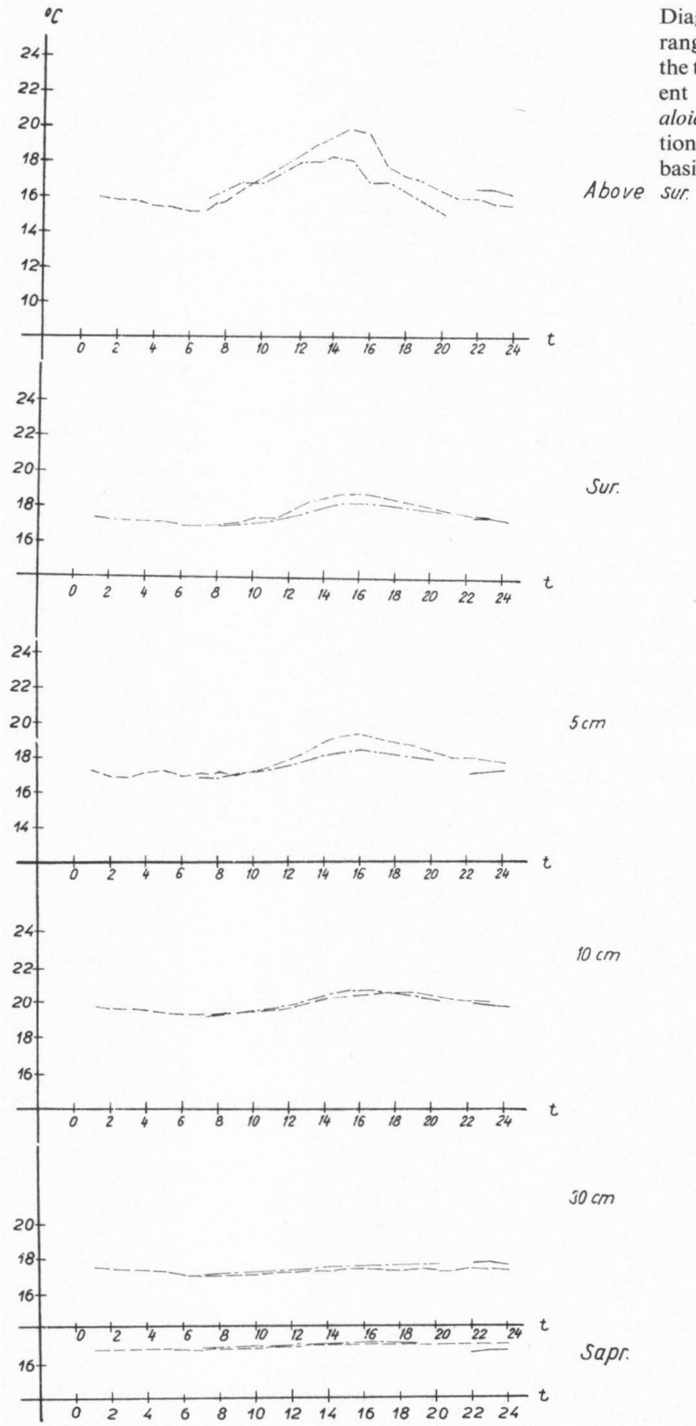




Diagr. 4. Examples of range and fluctuation of the temperature on different days in *Stratiotes aloides* vegetation in the Venematen basin.

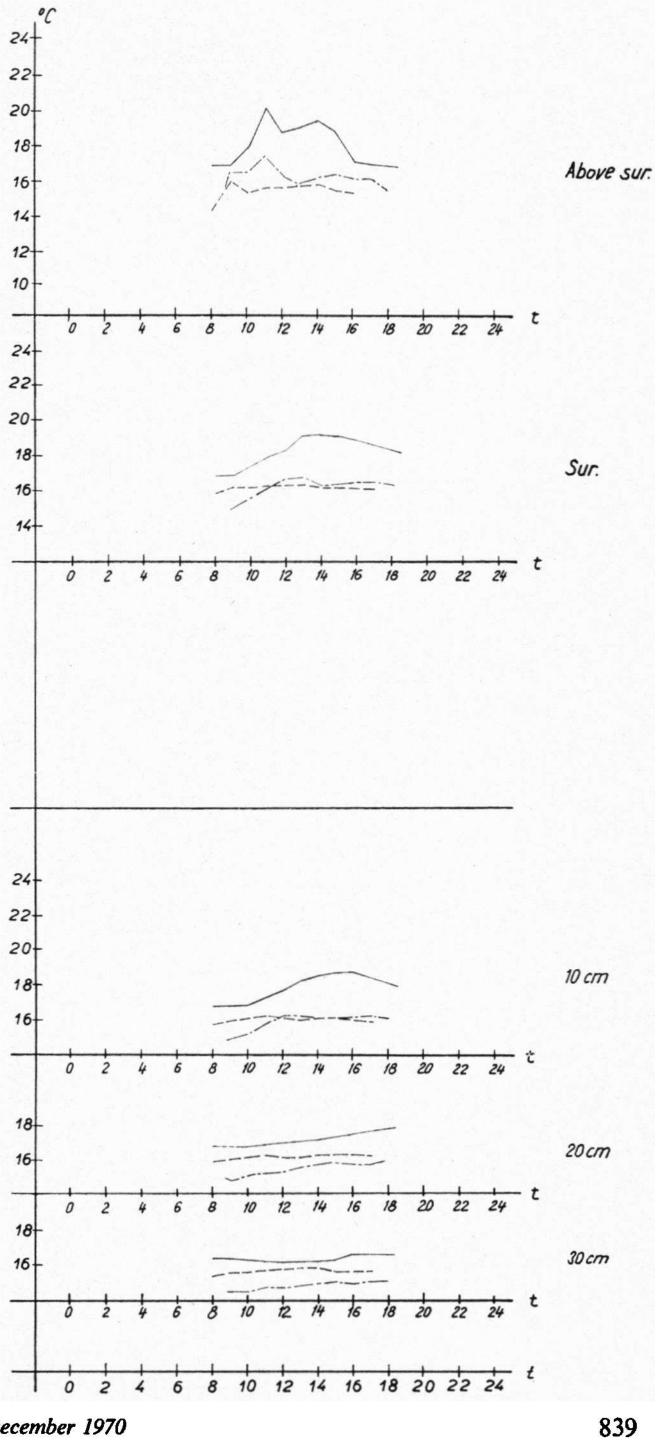
Diagr. 5. Examples of range and fluctuation of the temperature on different days in *Stratiotes aloides* vegetation in the Venematen basin.

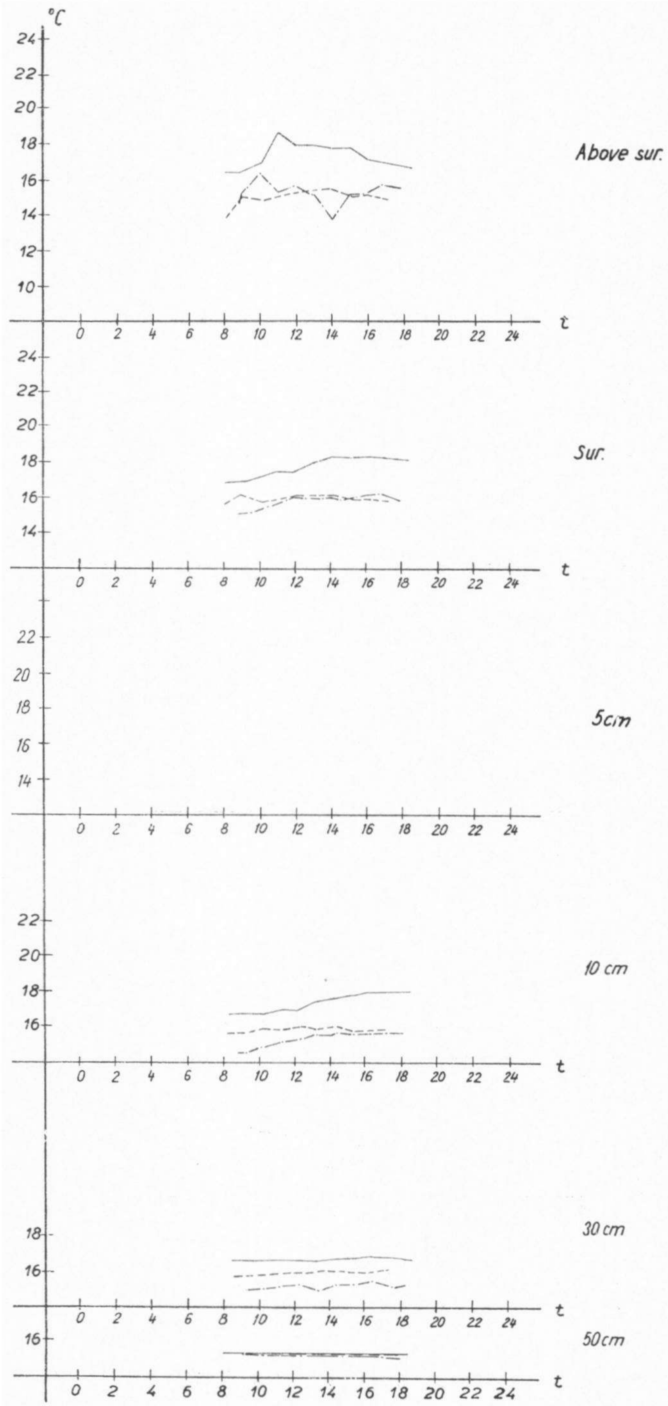




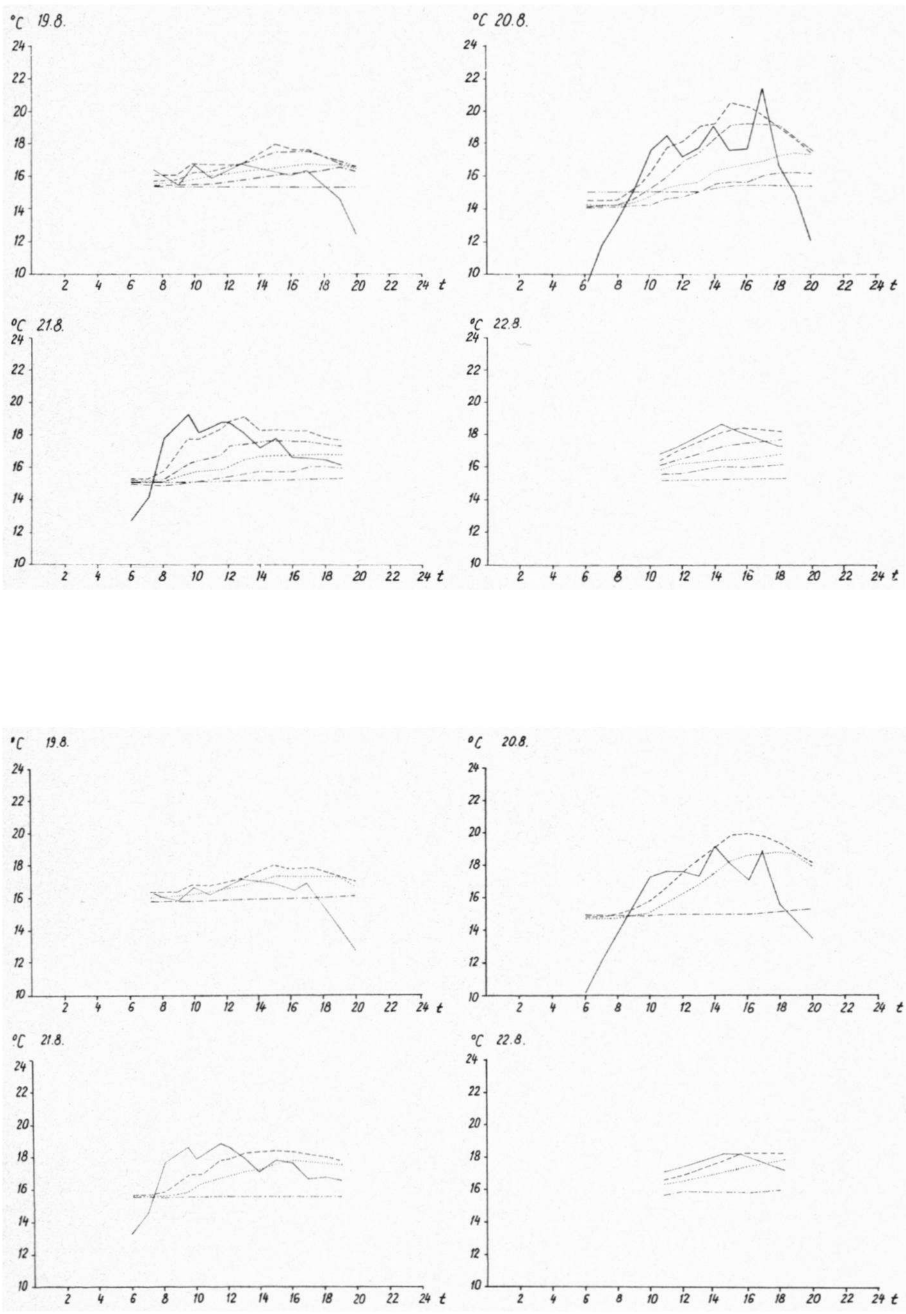
Diagr. 6. Examples of range and fluctuation of the temperature on different days in *Stratiotes aloides* submerged vegetation in the Venematen basin.

Diagr. 7. Examples of range and fluctuation of the temperature on different days in *Stratiotes aloides* vegetation in the Zuideindigerwiede basin.

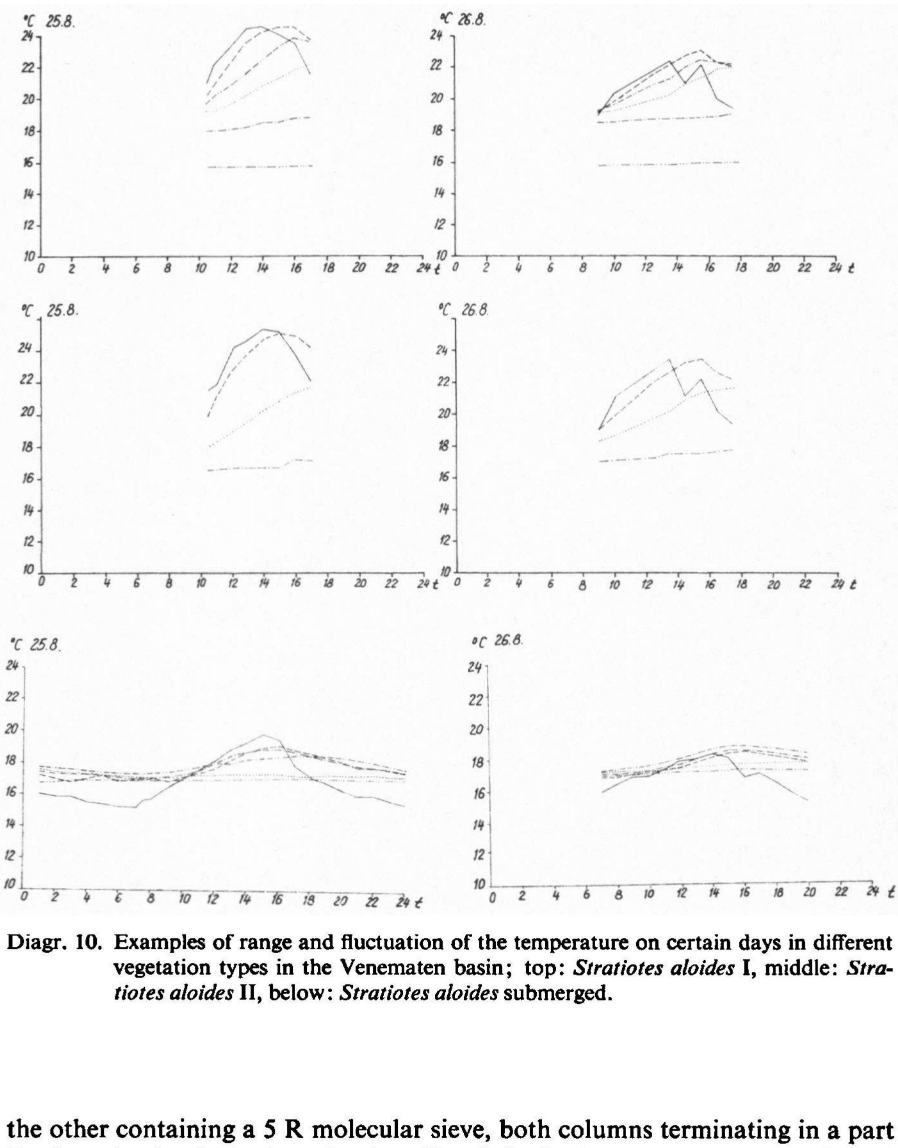




Diagr. 8. Examples of range and fluctuation of the temperature on different days in mixed *Carex pseudocyperus* and *Carex paniculata* vegetation in the Zuideindigerwiede basin.



Diagr. 9. Examples of range and fluctuation of the temperature on certain days in different vegetation types in the Chielgat basin: at the left *Ceratophyllum demersum*, at the right *Stratiotes aloides* and *Phragmites communis*.



Diagr. 10. Examples of range and fluctuation of the temperature on certain days in different vegetation types in the Venematen basin; top: *Stratiotes aloides* I, middle: *Stratiotes aloides* II, below: *Stratiotes aloides* submerged.

the other containing a 5 R molecular sieve, both columns terminating in a part for detection by thermal conduction. Signals in the detector part were registered by an M 24 automatic recorder. The relative quantities of gases present in the mixtures were established from the characteristics of the peaks they produced in the recorder diagrams. The amounts of gaseous substances dissolved in the water layer just above the sapropelic sediment and in the layer just below the surface of the body of water were also determined, their quantities being estimated by means of a gas chromatograph with attached apparatus for analysis of water samples.

3. EXPERIMENTAL RESULTS AND DISCUSSION

3.1. Chemical characteristics of the sapropelic deposits

The chemical characteristics of the sapropelic sediments in the three lakes under investigation are shown in *table 1* to *6*. In *table 7* the mean values of the individual characters are plotted for each of the lakes.

Tables 1, 3 and *5* show dry matter content, total C and total N percentage of the mineral residue in the dry matter, and the exchangeable ions Ca^{++} and Mg^{++}; *tables 2, 4,* and *6* show the types of humic substances in the samples.

Table 1, relating to the Chielgat, shows that in this rather eutrophic lake, artificially made by peat digging, the sample from the *Ceratophyllum demersum* zone is rather anomalous, but the corresponding *table 2* does not show anomalous figures. *Tables 3* and *4*, of the also rather eutrophic Venematen area situated in an agricultural area, show a considerably higher quantity of dry matter with a lower C content and also a somewhat different character of the humus fractions. The Zuideindigerwiede (*tables 5* and *6*) is the most oligotrophic of the three and has a sandy subsoil, but is much more of a recreational area than the other two. Dry matter content of the sapropelic sediment is about 30 per cent., but the quality of the humus fractions is slightly different from the other two areas.

Table 7 summarizes the means of the values obtained and gives a good idea of the various trophic levels of the three basins as far as the chemical character is concerned. The results suggest that the quantities recorded in the Venematen area are well-balanced, whereas those from the Zuideindigerwiede exhibit the greatest fluctuation. The concentration gradients are sometimes rather steep even between sites lying fairly close to one another.

3.2. Temperature readings

The temperatures were measured at various depths, as mentioned before, in the various vegetational zones and on different days during the months of August and September.

In the Chielgat temperatures were taken in the zones of *Ceratophyllum demersum*, of *Stratiotes aloides*, and of *Stratiotes aloides* and *Phragmites communis* on August 19, 20, 21, and 22, 1967; in the Venematen lake in the zones of submerged *Stratiotes aloides* and emerged *Stratiotes aloides* in two different places on August 25 and 26, 1967; and in the Zuideindigerwiede in the *Stratiotes aloides* zone and in vegetation of *Carex pseudocyperus* and *C. paniculata* on September 2, 3, and 4, 1967. *(Diagr. 1* to *10).*

The temperature readings were evaluated in two different ways, *viz.* by recording the temperatures in each layer for all days so as to get some idea of the range of variation in the different layers of vegetation, and by recording the temperatures of all layers for each day separately so as to get an idea of the effect of daily fluctuations. The results thus obtained show that the temperatures of different layers of water are partly determined by the relative position and exposure of a zone of vegetation (*i.e.*, by the situation with respect to the wind-

Table 1. Some chemical characteristics of sapropels in various vegetation zones of the Chielgat basin.

Chielgat	percentage dry matter in fresh sample	percentage H_2O in air-dried sample	percentage ash in dry matter	percentage total C in dry matter	percentage total N in dry matter	Ca mg/100 g in dry matter	Mg mg/100 g in dry matter	Ca:Mg	C:N
14. Nuphar luteum + Typha angustifolia	9.09	12.40	0.14	97.40	1.99	1.587	610	2.60	48.90
15. Stratiotes aloides + Ceratophyllum demersum	12.77	12.00	13.68	84.50	1.77	1.574	460	3.42	48.00
16. Ceratophyllum demersum	9.93	9.00	46.70	31.70	1.05	1.088	436	2.49	30.30
17. Stratiotes aloides	8.35	11.60	5.46	92.20	1.81	1.470	436	3.37	51.00
18. Stratiotes aloides	7.92	12.40	5.36	93.10	2.42	1.541	335	4.60	38.50
19. Stratiotes aloides + Phragmites communis	7.69	29.00	8.94	88.60	2.46	1.688	358	4.71	36.04
20. Utricularia vulgaris	8.45	10.00	13.72	83.70	2.33	1.545	371	4.16	36.00

Table 2. Some characteristics of the humus of sapropels in various vegetational zones of the basin Chielgat.

Chielgat:	FHS blue	FHS red	FHA	FFA	SHS	KZ	FS	FH_1	FH_2
14. Nuphar luteum + Typha angustifolia	1.50	0.18	1.425	0.075	0.860	8.33	0.57	0.95	19.00
15. Stratiotes aloides + Ceratophyllum demersum	1.70	0.18	1.170	0.530	0.645	9.44	0.39	0.70	2.20
16. Ceratophyllum demersum	1.40	0.14	1.373	0.025	0.725	10.00	0.51	0.98	55.00
17. Stratiotes aloides	1.80	0.22	1.550	0.250	0.660	8.18	0.36	0.86	6.20
18. Stratiotes aloides	1.80	0.22	1.600	0.200	0.800	8.18	0.44	0.89	8.00
19. Stratiotes aloides + Phragmites communis	1.27	0.22	1.225	0.050	0.545	5.64	0.43	0.96	24.50
20. Utricularia vulgaris	1.50	0.30	1.275	0.225	1.300	5.00	0.86	0.85	5.65

FHS = free humic substances
FHA = free humic acids
FFA = free fulvic acids
SHS = sorbed humic substances

KZ = E FHS bleu/E FHS red
FS = E SHS/E FHS
FH_1 = E FHA/E FHS
FH_2 = E FHA/E FFA

Table 3. Some chemical characteristics of sapropels in various vegetational zones of the Venematen basin.

Venematen	percentage dry matter in fresh sample	percentage H_2O in air-dried sample	percentage ash in dry matter	percentage total C in dry matter	percentage total N in dry matter	Ca mg/100 g in dry matter	Mg mg/100 g in dry matter	Ca:Mg	C:N
1. Open water Potamogeton lucens + Elodea nuttallii	19.30	8.00	57.19	41.50	1.33	636	291	2.18	31.20
2. Open water Nuphar luteum + Typha angustifolia	18.87	5.00	55.23	43.40	1.54	511	324	1.58	28.40
3. Stratiotes aloides submerged	19.34	14.60	53.82	44.70	1.45	591	329	1.78	30.80
4. Stratiotes aloides border submerged/emerged	21.19	6.40	66.80	32.00	1.41	525	239	2.19	22.80
5. Stratiotes aloides + Hydrocharis morsus-ranae	20.79	8.00	56.22	42.60	1.27	680	332	2.05	33.50
6. Cicuta virosa floating island	23.78	6.00	59.07	39.50	1.33	562	315	1.78	29.60
7. Nymphoides peltata	19.86	4.60	60.78	37.90	1.47	632	411	1.54	25.80
8. Nymphaea alba + Nuphar luteum	20.14	7.80	59.26	39.20	1.34	788	324	2.43	29.30
9. Stratiotes aloides canal	15.90	5.80	54.93	43.28	1.70	605	425	1.42	25.30

Table 4. Some characteristics of the humus of sapropels in various vegetational zones of the basin Venematen.

Venematen	FHS blue	FHS red	FHA	FFA	SHS	KZ	FS	FH_1	FH_2
1. Open water Potamogeton lucens + Elodea nuttalli	1.30	0.125	1.300	–	–	10.40	–	1.00	–
2. Open water Nuphar luteum + Typha angustifolia	1.45	0.150	1.450	–	0.605	9.66	0.41	1.00	–
3. Stratiotes aloides submerged	1.50	0.150	1.400	0.10	0.740	10.00	0.49	0.93	14.00
4. Straitiotes aloides border submerged/emerged	1.00	0.090	0.960	0.04	0.485	11.11	0.48	0.96	24.00
5. Stratiotes aloides + Hydrocharis morsus-ranae	1.50	0.195	1.425	0.10	0.715	7.69	0.47	0.96	57.00
6. Cicution	1.10	0.097	1.060	0.04	0.560	11.34	0.51	0.96	26.50
7. Nymphoides peltata	1.25	0.120	1.200	0.05	0.595	10.41	0.47	0.97	24.00
8. Nymphaea alba + Nuphar luteum	0.95	0.125	0.770	0.18	0.610	7.60	0.64	0.81	4.27
9. Stratiotes aloides	1.50	0.160	1.225	0.27	0.640	9.37	0.42	0.82	5.44

FHS = free humic substances
FHA = free humic acids
FFA = free fluvic acids
SHS = sorbed humic substances

KZ = E FHS blue/ E FHS red
FS = E SHS/E FHS
FH_2 = E FHA/E FHS
FH_2 = E FHA/E FFA

Table 5. Some chemical characteristics of sapropels in various vegetational zones of the Zuideindigerwiede.

Zuideindigerwiede	percentage dry matter in fresh sample	percentage H_2O in air-dried sample	percentage ash in dry matter	percentage total C in dry matter	percentage total N in dry matter	Ca mg/100 g in dry matter	Mg mg/100 g in dry matter	Ca : Mg	C : N
10. Stratiotes submerged	13.25	7.50	54.60	44.10	1.33	1,180	335	3.52	33.20
11. Stratiotes aloides + Hydrocharis morsus-ranae	25.90	0.60	93.60	6.23	0.41	187	373		15.30
12. Utricularia vulgaris	35.44	1.40	77.82	22.00	0.56	148	226		39.20
13. Utricularia vulgaris	70.11	1.60	57.63	42.00	0.39	360	345	1.04	108.70
Kleine Zuideindigerwiede									
21. Stratiotes aloides	24.14		93.71	6.19	0.64	516	305	1.69	9.50
22. Nuphar luteum + Nymphaea alba	21.88	2.6	79.50	20.10	0.70	602	327	1.84	28.70

Table 6. Some characteristics of humus sapropels in various vegetational zones of the basin Zuidereindigerwiede.

Zuideindigerwiede:	FHS blue	FHS red	FHA	FFA	SHS	KZ	FS	FH_1	FH_2
10. Stratiotes submer.	–	0.280	1.325	–	–	–	–	–	–
11. Stratiotes + Hydrocharis morsus-ranae	1.05	0.125	0.905	0.145	0.905	8.400	0.45	0.86	6.24
12. Utricularia vulgaris	1.50	0.230	1.375	0.125	–	6.520	–	0.91	11.00
13. Utricularia vulgaris	0.87	0.110	0.755	0.115	0.545	7.910	0.62	0.87	6.74
21. Stratiotes aloides	1.15	0.120	0.765	0.385	0.255	9.580	0.22	0.67	1.98
22. Nuphar luteum +Nymphaea alba	1.45	0.195	1.125	0.325	0.695	7.430	0.48	0.78	3.46

FHS = free humic substances
FHA = free humic acids
FFA = free fulvic acids
SHS = sorbed humic substances

KZ = E FHS blue/E FHS red
FS = E SHS/E FHS
FH_1 = E FHA/E FHS
FH_2 = E FHA/E FFA

Table 7. Average values of chemical characteristics of sapropels in the basins under study.

Basin	Chemical character	percentage dry matter in fresh sample	percentage H_2O in air-dried sample	percentage ash in dry matter	percentage total C in dry matter	percentage total N in dry matter	Ca mg/100 g in dry matter	Mg mg/100 g in dry matter	Ca : Mg	C : N
Zuideindigerwiede		31.78	68.21	76.14	23.43	0.67	499	318	1.56	39.1
Venematen		19.88	80.10	58.03	40.45	1.43	621	332	1.88	34.1
Chielgat		9.17	90.80	13.40	81.60	1.98	1,499	429	3.62	41.2

Basin	Quality of hum. subst.	FHS	FHS	FFA	SHS	QZ	FS	FH_2	FH_2
Zuideindigerwiede		1.20	1.041	0.296	0.495	7.97	0.44	0.83	5.88
Venematen		1.29	1.198	0.111	0.618	9.73	0.486	0.93	22.17
Chielgat		1.57	1.374	0.193	0.790	7.82	0.508	0.88	17.22

Table 8. The average peak tops of various components of gas mixtures under and in the vegetational cover obtained from various vegetational zones of the Chielgat basin.

Vegetational zone	Under the vegetational cover				In the vegetational cover			
	CO_2	O_2	N_2	CH_4	CO_2	O_2	N_2	CH_4
Ceratophyllum demersum	1.55	0.47	5.02	5.34	3.52	2.90	16.45	0.75
Utricularia vulgaris	1.90	0.56	5.60	5.53	2.00	1.96	14.00	0.51
Stratiotes aloides submerged	1.60	0.44	5.96	5.43	1.81	2.61	11.70	1.41
Stratiotes aloides emerged	2.02	0.37	4.82	6.10	2.15	1.92	7.40	3.62
Stratiotes aloides + Phragmites communis	1.62	0.54	7.20	4.30	1.05	1.30	8.70	1.90

Tables 8, 9 and 10 give the average values of five to fifteen measurements in the vegetational zones on different days.

or lee-side, the insolation, the duration of the insolation, etc.) and partly by the structure of the local stand of vegetation (height, density, relative height in respect of the surface, *i.e.*, submerged, partly floating, or emerged, etc.) The daily fluctuations have a marked effect on the microclimatic conditions. This is obvious from the fact that on sunny days with a great deal of insolation the temperatures tend to be higher, while on cloudy or rainy days they are lower. Of considerable interest is the time-shift in the warming-up or cooling-down of the lowermost water layers as related to the layeis near the surface (as could be observed on days with changeable weather), and also a micro-inversion effect, the place of the layer with the highest temperature sometimes being determined by vegetational structure.

3.3. The composition of gas mixtures produced in and below the various vegetational zones

On the same days on which microclimatological data were assembled gas samples were collected in various vegetational zones and in the sapropelic deposits below each zone. *Table 8* shows the results of gas-chromatographic analysis of the samples from the Chielgat. It is quite clear that the composition of the gas mixture in the sapropelic deposit differs appreciably from that of the aquatic habitat above it: while in the sapropels the O_2 content is very low and the CH_4 content relatively high, in the vegetation stands the O_2 content is higher, the CH_4 content much lower and even the N_2 content is higher than in the sapropels. Various vegetational zones differ more in the gaseous components of the aqueous medium than in the composition of the sapropel gases. *Table 9* shows the peaks corresponding to the components of the gas mixtures obtained from the sapropels and from the vegetational zones in the Venematen. The conditions below a floating island with *Cicuta virosa* are more anaerobic than under a cover of *Stratiotes aloides* vegetation. Judging by the amounts of CO_2 and CH_4, the decomposition cf organic substances also proceeds at a faster rate under the floating islands. As compared to the conditions at the Chielgat, the amount of N_2 is greater and the amounts of CO_2 and CH_4 are smaller under the *Stratiotes aloides* cover.

Table 10 shows the composition of the samples from the Zuideindigerwiede. The conditions in the vegetation stand appear to be very much the same as those

Table 9. The average peak tops of various components of gas mixtures under the plant cover obtained from various vegetational zones of the Venematen basin.

Vegetational zone	Under the plant cover			
	CO_2	O_2	N_2	CH_4
Stratiotes aloides	1.07	2.50	6.94	3.94
Cicuta virosa floating island	1.53	1.70	6.78	5.98

Tables 8, 9 and 10 give the average values of five to fifteen measurements in the vegetational zones on different days.

Table 10. The average peak tops of various components of gas mixtures under and in the vegetational cover obtained from various vegetational zones of the Zuideindigerwiede basin.

Vegetational zone					In the vegetational cover			
	CO_2	O_2	N_2	CH_4	CO_2	O_2	N_2	CH_4
Stratiotes aloides emer.	2.93	1.03	3.57	6.80	1.35	1.77	11.32	2.81
Utricularia vulgaris	3.61	0.69	2.33	7.39	1.35	3.71	11.95	0.86
Floating island Cicuta virosa + Carex pseudocyperus + Carex paniculata	2.01	0.87	3.66	7.22				

Tables 8, 9 and 10 give the average values of five to fifteen measurements in the vegetational zones on different days.

Table 11. The average tops of the peaks of various components of the mixture of mud gases in the basins under study.

	CO_2	O_2	N_2	CH_4
Chielgat	1.74	0.47	5.72	5.34
Venematen	1.30	2.10	6.86	4.96
Zuideindigerwiede	2.85	0.86	3.19	7.14

prevailing in the Chielgat, but the N_2 content found in the water was appreciably higher than that found in the sapropel layer in the Chielgat, and the O_2 content was also higher in the stands of *Utricularia vulgaris* vegetation.

Table 11 gives a summary of the conditions prevailing in the sapropelic sediment in all the three sampling areas. The highest CO_2 and CH_4 contents were recorded in the Zuideindigerwiede and the lowest in the Venematen where, on the other hand, the free N_2 content was the highest.

In *table 12* an attempt is made at showing the relative amounts of CO_2 and CH_4 (products of C-metabolism) and of N_2 (the end product of N-metabolism) released from the ecosystem in different vegetational zones in all the three areas under study. The last column of this table shows the ratio C:N in the zones of all basins and the average value of this ratio in the lakes. The high and relatively inconstant C:N ratio in the mud gases in the Zuideindigerwiede is in contrast with the much more constant C:N ratio in the other two sampling areas.

Finally, *table 13* represents the results of gas analyses, expressed as mean values of the quantities of all gases included in the investigation in the different zones of vegetation, both below and in the plant cover. There is apparently a relation between the composition of the gaseous components of the sapropelic deposit and of the local stand of aquatic vegetation: high methane content and low N_2 content in the sapropelic layer is concomittant with a relatively low CH_4 and a somewhat higher N_2 content among aquatic vegetation on the same site.

Table 12. Amount of gases and the C:N ratio freed from various vegetational zones of the Chielgat, Venematen, and Zuideindigerwiede basins.

Vegetational zone	CO_2+CH_4	N_2	C:N
Chielgat basin			Ø C:N = 1.27
Ceratophyllum demersum	6.89	5.02	1.37
Utricularia vulgaris	7.43	5.60	1.33
Stratiotes aloides submerged	7.03	5.96	1.18
Stratiotes aloides emerged	8.12	4.82	1.68
Stratiotes aloides + Phragmites communis	5.92	7.20	0.82
Venematen basin			Ø C:N = 1.13
Stratiotes aloides	5.01	6.94	0.72
Cicuta virosa floating island	7.51	6.78	1.55
Zuideindigerwiede basin			Ø C:N = 3.30
Stratiotes aloides	9.73	3.53	2.76
Utricularia vulgaris	11.0	2.33	4.72
Cicuta virosa + Carex pseudocyperus + Carex paniculata	9.23	3.66	2.52

Table 13. The average tops of the peaks of various components of the mixture of gases produced in the vegetational cover and under it in various vegetational zones of all the basins under study.

Vegetational zone	Under the vegetational cover				In the vegetational cover			
	CO_2	O_2	N_2	CH_4	CO_2	O_2	N_2	CH_4
Stratiotes aloides	2.27	1.44	5.13	6.00	1.50	1.80	10.58	2.96
Utricularia vulgaris	3.15	0.66	3.22	6.90	1.51	3.29	12.43	0.80
Cicuta virosa	1.82	1.19	5.25	6.82				

There is a rather striking difference between the gas composition in the vegetation with *Stratiotes aloides* and that in the vegetation with *Utricularia vulgaris*: the latter is characterized by high O_2 and N_2 contents and a very low CH_4 content, whereas the former has a relatively high CH_4 content. The concentration gradients are also different in the two types of vegetation. This is obvious from the different composition of the gaseous mixtures collected in the bottom sediment and among vegetation. The decreasing quantities of CO_2 and of CH_4 and increasing quantitites of O_2 and of N_2 in the plant cover are shown in *table 13*.

3.4. The analysis of gases dissolved in water

Water samples, both from the bottom and from the surface, were collected in the Venematen on August 25, 1967 and in the Zuideindigerwiede on September 4, 1967, and subsequently analyzed for the total amount of dissolved gases. The amount of dissolved gases is substantially higher in the bottom layer than it is near the surface. This may be partly attributed to differences in the temperature of the water in the two layers compared and partly to the fact that the bottom

Table 14. The tops of the peaks of gases dissolved in water.

	Surface	Bottom
25. 8. Venematen		
Stratiotes	3.2	4.1
	2.4	3.5
	2.6	6.8
Ø =	2.8	5.6
4. 9. Zuideindigerweide		
Stratiotes	3.2	5.6
	4.2	3.5
	3.1	4.5
Ø =	3.5	4.4.

water is in diiect contact with the gas-producing environment below it (the gases are actually dissolved in it under pressure) whereas the uppermost water layer is subject to the activities of vegetation. The two days selected for the analyses strikingly differed meteorologically, as shown in the microclimatic records: on August 28 the weather was fair and bright with a marked microclimatological effect on the watery environment, whereas on September 4 the weather was dull and its effect on the water temperatures almost negligible. The meteorological differences between the two days also had considerable bearing on the actual difference between the amounts of gas near the bottom and near the surface (as shown in *table 14*) which were, expressed as mean values, 5.6 and 2.8 respectively, on August 28, and 4.4 and 3.5 respectively, on September 4.

The daily variations in the total amount of dissolved gases near the bottom and near the surface (as plotted in *table 14*) and the temperature ranges of the different layeis of water suggest that the alternation of gradual warming-up and cooling-down of water layers acts as a mechanism for the release of part of the mud gases. During the course of a day the uppermost water layers aie warmed up first, and the concentration of dissolved gases decreases accordingly by the diffusion of gases into the atmosphere. Subsequently, the upper water layer cools off again and the lower layers are gradually warmed up. This results in the diffusion of gases into the cooler upper layers, owing to a concentration gradient between the upper and the lower water layers. This process progresses downwards and involves lower layers of water, until it reaches the bottom layer and the temperature remains more or less constant. This is possibly the mechanism by which part of the gaseous components released from the sapropelic sediment passes through the water at unequal rates according to their specific solubility in water at different temperatures and in relation to the successive daily warming-up and cooling-off of the layers of water.

4. CONCLUSIONS

1. Properties of the substrate

Some chemical features of sapropels in the three basins of Chielgat, Venematen and Zuideindigerwiede were determined. The sapropels of Chielgat are characterized by a high percentage of carbon compounds, high contents of water, low dry weight, and extremely low ash contents. As shown by its low colour quotient and high factor of stabilization, the humus of the sapropels in Chielgat is very old. The content of calcium in the sapropels is extremely high. These features of the sapropels are probably due to the character of the basins. The sapropels cover a layer of peat several metres deep, and have no direct contact with the mineral subsoil substrate.

The dry weight content of the sapropels of Venematen is about 20%. In comparison with Chielgat, the sapropels of Venematen are characterized by a far larger amount of mineral substances and by much less carbon and nitrogen, while the content of calcium in the sapropels is much lower. Of the C:N ratios in the sapropels of all basins under study, the most favourable one can be found in the Venematen basin. This ratio and, consequently, very good trophism of this basin may be due to the position of the Venematen basin in an agricultural area. Very intensive agriculture, especially the application of high amounts of nitrogen fertilizers, may influence the level of nitrogen content in the basin and in the sapropels.

On the other hand, the trophic level of the Zuideindigerwiede basin is the worst of all three basins under study: high content of mineral substances, low content of C and N, and pronounced differences in the quality of sapropels in not too distant sites, and high ratios of C:N. All these features are due to the sandy subsoil and high mineralization rates in the basins.

2. Microclimatic conditions

The temperature readings in different air and water layers were realized in different vegetation zones in the three basins under study. The results obtained show that the microclimatic effect is partly determined by the relative position and exposure of the vegetation zone (i.e. exposure to the wind or lee-side, the insolation, the duration of insolation, etc.), partly by the structure of the plant cover (its height, density, whether it is submerged, partly floating or emerged, etc.).

3. Sapropel metabolism

The qualitative and quantitative chemical properties of sapropels and the composition of mud gases in different basins or habitats enable us to draw certain conclusions about the C and N metabolism taking place in the habitats of macrophyte vegetation in the basins under study. During our investigations, the differences between the composition of gases in macrophyte rhizosphere on the bottom and of gases in macrophyte vegetation under the water surface were estimated.

While in the mud gases on the bottom CH_4 is the principal part of the gas mixture, N_2 and O_2 prevail in the gas mixture from the plant cover. The photosynthesis taking place in plants is responsible for the high content of O_2.

The anaerobic cellulose decomposition processes taking place in the bottom layer are responsible for the high content of CH_4. The amounts of $CO_2 + CH_4$ on the one hand and the amount of N_2 on the other hand correspond to the outputs of C and N turnovers taking place in the basins. The gaseous outputs of C and N metabolisms in the basins under study are related to the C and N contents of individual basin sapropels. The amounts of gases dissolved in water from the bottom and from the surface were estimated. The amount of dissolved gases is substantially higher in the water from the bottom layer than in the water from the surface layer.

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