VERTICAL DISTRIBUTION OF BIOLOGICAL ACTIVITY IN PEAT OF SOME VIRGIN AND DRAINED SWAMP TYPES

ERKKI LÄHDE

HELSINKI 1966

Contents

Suomalaisen Kirjallisuuden Kirjapaino Oy Helsinki 1966

Introduction

The activity of peat-decomposing microbes is limited by many ecological factors. One of these is the oxidation-reduction ratio of the peat. The oxidation-reduction potential decreases from the soil surface downwards (ISOTALO 1951, PAARLAHTI 1961). In anaerobic conditions, the activity of decomposing microbes is suppressed. However, there are differences between tree species in their tolerance of anaerobic conditions. Of birch, spruce, and pine, birch seems to be most tolerant of these conditions (HUIKARI 1954). The oxygen supplying capacity of peat is, however, a site factor affecting the success of trees and in correlation with for instance the mobility of the water in the medium (HUIKARI 1954).

The draining of swamps has aimed at improving their water economy so that it would be more favorable also for microbial activity. MULTAMÄKI (1952), for instance, stressed the importance of oxygen availability in the decomposition of peat. The positive effect of drainage does not, however, extend beyond a thin surface layer even when the drains are placed close to each other (HUIKARI 1953, PAARLAHTI 1961). Thus the biologically active layer in both virgin and drained swamps is composed only of a thin surface layer (PAARLAHTI 1961).

This biological activity of peat has been relatively little studied by released and consumed gas quantities, although corresponding measurements have been made on raw humus in both field and laboratory conditions. Several methods have been tried for this purpose (ROMELL 1932). VIRO (1955) used a weight-analytical method in the determination of CO_2 release in litter under laboratory conditions. SIRÉN (1955) and ELKAN and MOORE (1962) used volume analytical methods. Gas volumetric measurements of CO_2 release in the field were made among others by ROMELL (1922) and LUNDEGÅRDH (1924). Colorimetric methods were also tried in these measurements (KOEPF 1953, FRERCKS 1954).

The methods listed above have made possible only the measurement of CO_2 release in decomposition. The so-called Warburg method makes possible (UMBREIT *et al.* 1951) also the measurement of the O_2 uptake in gas exchange. Such a method has been used in studying soil respiration (ROVIRA 1953, CHASE and GREY 1953, MEYER 1959 and 1960), and in the decomposition of litter (HINTIKKA 1964).

The decomposition rate in the soil *in situ* has been studied e.g. with cellulose as the study material. RICHARD (1945) carried out decomposition experiments with viscose silk thread as the material, and described the decomposition degree by the decrease in the tensile strength. In a study on the microbe species decomposing cellulose, TRIBE (1957) found a method good, in which cellulose pieces were kept in the soil for a certain period of time. The decomposition rate of cellulose at different depths in the soil can be measured from the decreased weights of such cellulose pieces (PAARLAHTI 1964, LÄHDE 1966).

The objective of this project is to determine the amount of gas exchange in peat samples taken from several swamps, using the Warburg method in the laboratory for the measurements. Special attention was directed toward the influence of the lowering of the ground water level through drainage, on oxidation-reduction conditions in the samples from both forested and treeless swamps. This determination was made by measuring oxygen uptake and carbon dioxide release. The biological activity *in situ* was determined by the cellulose decomposition rate method in the same plots from which the laboratory samples were taken.

Study objectives and methods

This project has been carried out in the Forestry Field Station of Helsinki University (200 km north of Helsinki) in the summers of 1964 and 1965. For the first summer field work, the sample plot pairs chosen were (1 a) a virgin open swamp (OCS) and (1 b) a swamp drained about fifteen years ago, originally of the same type as above (OCSdr 1), and (2 a) a *Myrtillus* spruce swamp (Myrt.SS) and (2 b) a very old (primarily either Myrt. SS or herb-rich spruce swamp) drained area (Myrt.dr 3, drained in 1913). In the second summer only a single sample plot pair was selected, and consisted of a low-sedge swamp (LCS) in contrast to an ordinary sedge swamp drained about 1925 (OCSdr 2). The tree stand data are given in table 1.

Table 1. Stand data from the sample plots.

Sample plots by swamp type[1]	Age of stand, years	Volume, cu.m/ha	Proportion of stems by species, %		
			Pine	Spruce	Birch
OCS		treeless			
OCSdr 1	15	10	50	10	40
Myrt. SS	65	85		70	30
Myrt.dr 3	95	160		100	
LCS		treeless			
OCSdr 2	40	115	100		

[1] OCS ordinary sedge swamp
LCS low-sedge swamp
Myrt.SS *Myrtillus* spruce swamp
OCPS ordinary sedge pine swamp
OCSdr 1 recently drained ordinary sedge swamp
OCSdr 2 drained ordinary sedge swamp with considerable site changes after draining
Myrt.dr 3 drained area with vegetation resembling that of a upland site, *Myrtillus*-type
Vacc.dr 3 drained area with vegetation resembling that of a upland site, *Vaccinium*-type

Table 2. Peat type and humification degree (H) of the peat layers in the sample plots.

Peat layer cm	Sample plots					
	OCS[1]	OCSdr 1	Myrt. SS	Myrt. dr 3	LCS	OCSdr 2
0— 3	S[2], H_2	MS + l[3], H_3	S + l, H^2	l,	S, H_1	S + l, H_1
5— 8	S , H_2	MS + l, H_3	MS + l, H_2	MC, H_7	CS, H_2	S + l, H_2
10—13	CS, H_2	MC, H_3	MC, H_5	MC, H_8	CS, H_2	CS, H_3
15—18		MC, H_6	MC, H_7	MC, H_8		CS, H_3
20—23		MC, H_5	MC, H_6	MC, H_8		CS, H_3
25—28		MC, H_5	MC, H_8	MC, H_8		MC, H_3

[1] See footnote on page 4
[2] S = *Sphagnum* peat
CS = *Carex-Sphagnum* peat
MS = Woody-*Sphagnum* peat
MC = Woody-*Carex* peat
[3] + 1 = litter

A Warburg apparatus model V 85 (manufacturer B. Braun, Melsungen) was used in the laboratory experiments. The peat samples were taken from the sample plots from ten randomized points with a special square sampling tube (5 cm × 5 cm in cross section). Samples were taken by layers three-cm in thickness, starting from the surface down to a depth of 28 cm, and leaving a two-cm layer between the individual sampled layers. The open-swamp plots were studied in layers only to the depth of 15 cm from the surface, the watery characters of the peat in the deeper layers making the extraction of a satisfactory sample impossible with the available tube. The peat type and the humification degree of each layer were determined according to von Post's method (table 2).

The ten samples taken from the same layer in any given plot were combined and mixed to form one composite sample as homogenous as possible; any large pieces of undecomposed wood that might interfere later with placing the peat into the flasks were removed from the samples.

From each composite sample, four subsamples, each with a fresh weight of one gram, were then placed into Warburg flasks. The apparatus took 14 flasks at a time; thus three different samples could be run simultaneously, allowing for two empty flasks to be used as thermobarometers connected to the manometers. Two ml of distilled water were added to the flasks containing the sample. Two-tenths ml of 10 % KOH solution and a piece of filter paper to absorb the released CO_2 were placed into the central well of the two flasks used for measuring O_2 uptake.

Respiration was measured during two hours and calculated as μl per gram of fresh peat per hour (μl/g/h). When it was impossible to examine all samples immediately, they were stored in a refrigerator at a temperature of ca. 5° C. All samples were processed during the day they were lifted. It was assumed that the time interval involved did not materially affect the oxidation-reduction determinations.

In investigating cellulose decomposition *in situ*, a method was used that had been found satisfactory by both PAARLAHTI (1964) and LÄHDE (1966). Cellulose pieces (3 × 5 × 0.15 cm) were placed vertically into peat in nylon-net bags. During both summers, they were kept in the swamp for almost four months, from the middle of June to the beginning of October. The decrease in the cellulose dry weight indicated the decomposition rate at various depths in the peat.

CO_2 release in peat samples taken from different depths in the swamp

The data given in table 3 are averages of CO_2 release from samples taken at four different times during the summer of 1964. The averages for the sample plot data in this study have been calculated on the assumption that variation in these plots during the summer was also quite similar, since the ground water level, rains and temperature have a similar effect in different sample plots at any given time (HEIKURAINEN and SEPPÄLÄ 1963). It should be emphasized, as previously pointed out by HEIKURAINEN *et al.* (1964), that the moisture content of peat depends on the variation of the ground water level.

The possible differences between the averages for layers and sample plots have been studied by the analysis of variance and F-test, and the least significant difference (LSD) has been calculated by Tukey's equation. Corresponding results for the summer 1965 data are given in table 4 as averages of four measurements.

Table 3. CO_2 release μl/g/h by layer and sample plot.

Depth cm	OCS	OCSdr 1	F	LSD.05	Myrt. SS	Myrt.dr 3	F	LSD.05	All sample plots F	All sample plots LSD.05
0— 3	12.73	39.48	71.50***	7.75	53.09	54.44	0.71	15.85	28.83***	15.16
5— 8	7.81	15.16	1.83	13.32	22.43	20.05	0.22	12.87	2.35	15.88
10—13	8.90	11.12	0.14	14.81	16.05	11.04	1.22	11.11	0.65	15.88
15—18		7.46			12.55	9.80	0.31	12.49	0.75	11.73
20—23		5.39			6.52	5.43	0.17	7.34	0.09	9.12
25—28		8.89			7.09	7.91	0.03	9.55	0.09	11.42
F	0.79	14.22***			18.42***	48.79***				
LSD.05	11.53	15.12			18.27	11.93				

In the laboratory experiments, the CO_2 release was considerably greater in samples taken from the surface layers of the swamp than in samples taken deeper (tables 3 and 4). From open swamps, samples were taken only from the surface layers; between these, no statistically significant differences can be seen. The surface layer (0—3 cm) in Myrt.SS and in Myrt.dr 3 differs most from the other

Table 4. CO_2 release μl/g/h by layer and sample plot.

Depth cm	LCS	OCSdr 2	F	LSD.06
0— 3	9.22	41.88	22.94***	16.71
5— 8	10.04	43.37	36.41***	13.53
10—13	12.37	30.04	9.06*	13.98
15—18		11.92		
20—23		17.32		
25—28		12.65		
F	0.81	5.75*		
LSD.05	8.33	26.82		

layers, and even the 5—8 cm layer considerably from the layers deeper than 20 cm; in OCSdr 1 the deeper than surface layers do not differ from each other as clearly. This last-mentioned sample plot has been drained and afforested only ca. 15 years ago. Drainage and the tree stand have changed the ecological conditions on which microbial activity depends. The OCSdr 2 sample plot (table 4), primarily of the same type as OCS and OCSdr 1, has been drained much earlier. The peat samples taken from the surface layers (0—15 cm) do not, in this plot, differ from each other in respect to the CO_2 release, but do differ from the samples taken from deeper layers. In the light of the laboratory experiments, it is apparent that the effect of draining on the biological activity of peat in this sample plot extends deeper than in the other sample plots.

A difference between the sample plots exists also, when the CO_2 release of the samples taken from the surface layers of the open swamps and of the comparable drained swamps are compared. The CO_2 release in the forested plots is greater than in the open swamps. The CO_2 release of the surface layers in open swamps is of the same magnitude as that of the layer deeper than 10 cm in the forested swamps.

Proportions of the O_2 uptake and CO_2 release

As has already been seen, the Warburg apparatus could be used in the simultaneous measurement of O_2 uptake and CO_2 release in the peat samples. In normal conditions, the number of O_2-molecules consumed in the oxidation of organic substances is about the same as the number of released CO_2-molecules; in other words, the quantity ratio of these gases is approximately 1. However, when the sample studied is in partly or totally anaerobic condition and gets into contact with free oxygen, it is postulated that an oxidation reaction occurs, in which a corresponding amount of carbon dioxide is not released.

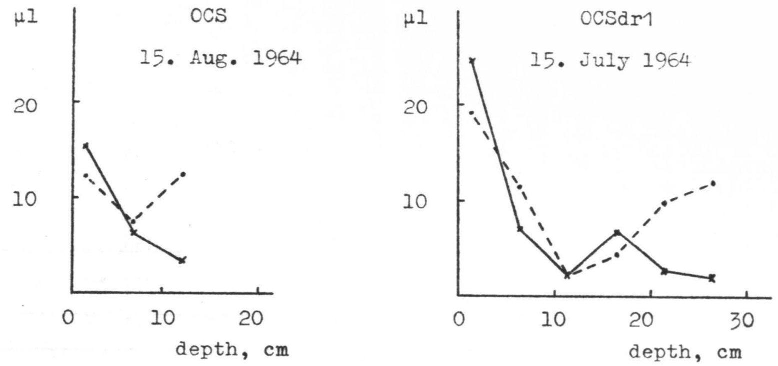

Figure 1. CO_2 release (——) and O_2 uptake (- - - -) (μl/g/h) in peat samples taken from different depths.

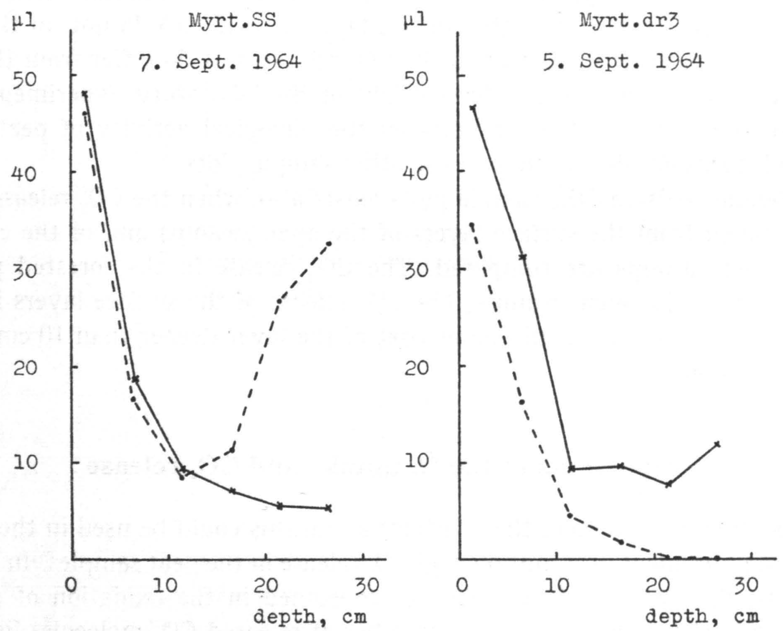

Figure 2. CO_2 release (——) and O_2 uptake (- - - -) (μl/g/h) in peat samples taken from different depths.

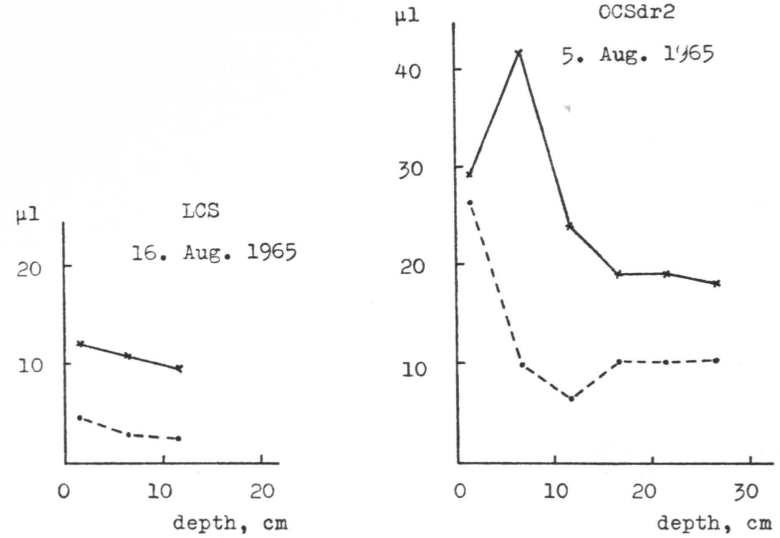

Figure 3. CO_2 release (——) and O_2 uptake (- - - -) (μl/g/h) in peat samples taken from different depths.

With this hypothesis as the basis, the reaction of peat samples, taken from different conditions at different depths was studied in the presence of free oxygen in the Warburg apparatus. Examples of the results of these measurements are given in figures 1—3. They show, by sample plot pairs, the oxygen consumption and the carbon dioxide release of samples taken from different depths. For these measurements, samples were taken 7—8 times in the summer of 1964, and 4—5 times in the summer of 1965. Figure 2 shows the decrease from the surface downwards of both the CO_2 and O_2 quantities in the Myrt.dr 3 samples. The situation was different in the Myrt.SS (figure 2). The CO_2 quantity decreased here, also, but the O_2 uptake curve for the samples has a turning poirt between the depths of 10 and 20 cm, and then rises again. This could be seen in both the open-swamp and other drained-swamp sample plots.

The turning point, at which the oxygen uptake starts to rise, changes during the summer and is characteristic of any given sample plot; it seems to coincide with the changes in the groundwater level (figures 4 and 5).[1] An accurate point can not be determined by measurements; this is due the fact that the samples have been taken from relatively thick layers (3 cm), and the part of the peat between layers (2 cm) has not been studied.

[1] The ground water level fluctuation data are from the Helsinki University Department of Peatland Forestry, from measurements made under the direction of Professor Heikurainen.

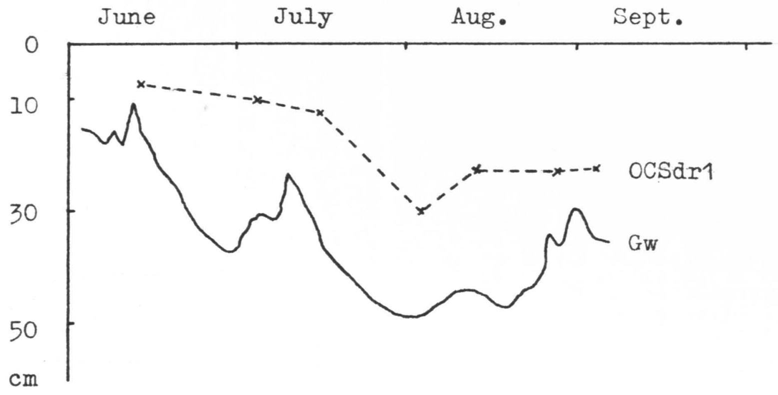

Figure 4. The turning point in the OSCdr 1, calculated on the basis of the CO_2 release and the O_2 uptake, and the changes of the groundwater level (Gw) during the summer of 1964.

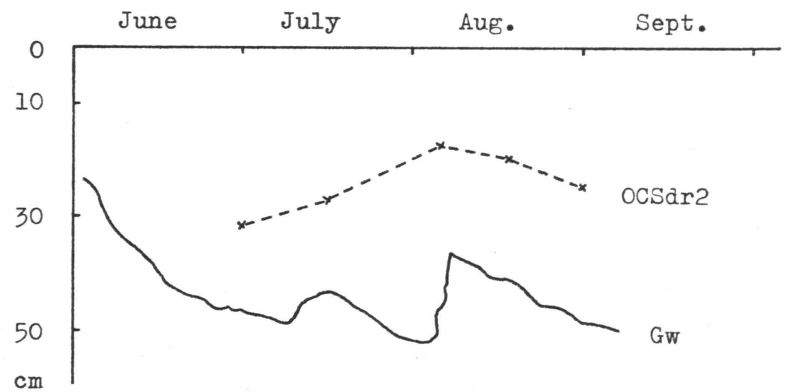

Figure 5. The turning point in the OCSdr 2, calculated on the basis of the CO_2 release and O_2 uptake, and the changes of the groundwater level (Gw) during the summer of 1965.

Rate of cellulose decomposition

The cellulose decomposition rate at different depths in peat was measured from the same sample plots as were used for the Warburg determinations. The results are given in tables 5 and 6. The summer of 1964 data (table 5) includes 10, and the summer of 1965 data (table 6) 20 pieces of cellulose per sample plot layer.

Table 5. Loss of dry weight of cellulose (per cent) during the summer of 1964.

Depth, cm	OCS	OCSdr 1	F	LSD.05	Myrt.SS	Myrt.dr 3	F	LSD.05
0—10	17.8	31.9	** 8.58	10.1	17.2	34.8	*** 25.13	23.3
10—20	3.2	18.0	** 11.29	9.2	2.5	25.0	* 5.40	20.3
20—30	0.4	10.2	* 6.67	7.9	0.7	19.6	* 5.52	16.8
30—40	0.5	0.8	0.82	0.6	1.0	11.6	2.93	13.0
40—50	0.2	—	3.33	0.3	1.1	7.1	2.06	8.8
F	*** 58.04	*** 19.48			*** 12.12		1.90	
LSD.05	4.0	12.2			8.3		32.2	

Table 6. Loss of dry weight of cellulose (per cent) during the summer of 1965.

Depth, cm	LCS	OCSdr 2	F	LSD.05
0— 5	14.4	22.6	** 9.08	5.4
5—10	3.8	7.1	3.94	3.5
10—15	0.2	4.7	** 9.24	2.7
15—20	0.1	6.5	16.28	3.1
20—25	0.1	6.6	*** 14.60	2.4
25—30	—	8.6	*** 16.27	2.9
F	*** 54.16	*** 14.20		
LSD.05	3.4	7.8		

The effect of drainage and the tree stand on the activity of decomposing microbes can be examined by sample plot pairs. The decomposition of cellulose slows down considerably with increasing depth in all of the virgin and recently drained areas. In contrast, in the Myrt. dr 3 it is considerable, even at the depth of 40—50 cm. However, in open swamps cellulose is decomposed only in the 0—10 cm layers, remaining essentially unaltered at lower depths. This is true also in the virgin, forested Myrt.SS. In this respect the results differ from those given by the Warburg measurements (tables 3 and 4).

In the virgin versus the drained sample plots a difference exists between the cellulose decomposition rate. It is faster in Myrt.dr 3, the OCSdr 2, and the

OCSdr 1 than in the corresponding undrained swamps. In the comparison of all the sample plots, decomposition proves to be the fastest in the drained area where the drainage has been most effective. This difference does not, however, have to be due to the extent of drainage, since the sample plots differ somewhat also in their peat type and their original swamp type.

Discussion

From the results, it can be seen that in the sample plots in open swamps, in the CO_2 release rate there are not consistent differences in the peat samples taken from different depths, but in the other sample plots rapid decreases are found with increasing depth (already at 5—8 cm). The decreased biological activity of peat is due to the oxidation-reduction conditions, which among other factors also cause shallow root systems and a decrease in microbe quantities with increasing peat depth (WAKSMAN and PURVIS 1932, PAARLAHTI 1961). The superficiality of the roots in a swamp is indicated by the distribution pattern of root tips at different depths (HEIKURAINEN 1955). A major portion, ca. 87 %, of the number of root tips was within the first 5 cm surface layer and only ca. 3 % in the layers below 10 cm.

The CO_2 release rate may also be increased by the respiration of tree roots, since there are no statistically significant differences among the CO_2 release rates for the 0—3 cm layer peat samples in the forested sample plots, but in the open swamps the rates are only ca. 1/3 of these (tables 3 and 4). There were no statistically significant differences among the CO_2 release rates of the OCS and LCS samples taken from different depths. The ground vegetation of these sample plots is composed mainly of *Sphagnum* mosses and sedges. The sedge roots extend largely beyond the depth of 10 cm (GYLLENBERG *et al.* 1955). PAARLAHTI (1961) has also found an equally large bacterial flora in the surface layer of Vacc. dr 3[1], Myrt.dr 3, OCPS, and Myrt.SS, but a much smaller one in that of treeless swamps.

In comparing the results of the cellulose *in situ* decomposition experiment and those from the Warburg measurements, the rate and the CO_2 release of the samples from different depths appear correlated. A difference in the results can be seen in the slower decomposition of cellulose in the Myrt.SS surface layer than in that of the corresponding drained swamp, as contrasted to the CO_2 release, which may at times be even greater in the samples taken from this depth. Thus the result indicates improved conditions for cellulose-decomposing microbes after draining.

The possibility also exists that the biological activity of peat after draining, as indicated by the CO_2 release, increases to a considerable depth in peat until the decreasing amounts of easily decomposable substances set a limit to this activity in an old drainage area, although the cellulose decomposition rate still increases with the improvement of the oxidation-reduction conditions. Changes in the oxidation-reduction conditions can be examined especially in the results of the Warburg measurements. With the apparatus, measuring the oxygen consumed in gas exchange has been feasible and thus it has been possible to notice the phenomenon reflected in this ratio. The method is based on the hypothesis that there are substances in peat, which in the presence of free oxygen are oxidized the faster the lower the oxidation-reduction potential originally in the swamp.

[1] See footnote on page 4

On the basis of the measurements made, such oxygen deficiency is not seen in the Myrt.dr 3 (figure 2), where the ground water level during the whole period of measurement has stayed below the 30 cm limit; both the CO_2 release and the O_2 uptake in the peat samples representing different depths have been of the same magnitude during the whole period of study. The situation has been different in the other sample plots. An especially marked oxygen deficiency slowing down decomposition can be seen in the Myrt.SS sample plot in the 10—13 cm and deeper layers. In the OCS the turning point, at which the amount of O_2 consumed exceeds the amount of CO_2 released, is quite close to the surface. A turning point can also be seen in the OCSdr 1 and the OCSdr 2 (figures 1 and 3). In these two sample plots, the groundwater level has occasionally been deeper than 28 cm.

Especially in the Myrt.SS, the OCSdr 1, and the OCSdr 2, the turning point can be seen to vary with time between measurements, apparently following groundwater level fluctuations (figures 4 and 5). The turning point rises with the groundwater level. On the other hand, rains may raise the groundwater level, but also carry oxygen into the swamp. In these respects, the results only indicate trends, but they do offer a reason to continue the experiments, using the Warburg method, especially to find a solution for the important oxidation relationship question in peat.

References

CHASE, F. E. and GRAY, P. H. H. 1953. Use of the Warburg respirometer to study microbial activity in soils. Nature (Lond.) 171: 481.

ELKAN, G. H. and MOORE, W. E. C. 1962. A rapid method for measurement of CO_2 evolution by soil micro-organisms. Ecology 43. 4: 775—776.

FRERCKS, W. 1954. Die Bodenatmung als Mittel zur Erfassung der Mikroorganismentätigkeit in Moor- und Heidesandböden, ein neuer Verfahren zu ihrer Bestimmung und erste Ergebnisse. Pflanzenern. u. Bodenkunde 66: 39—54.

GYLLENBERG, H., HANIOJA, P. and VARTIOVAARA, U. 1954. Havaintoja eräiden viljelemättömien maatyyppien mikrobiston koostumuksesta. Summary: Observations on the composition of microbial population in some virgin soils. Acta Forest. Fenn. 62. 2.

HEIKURAINEN, L. 1955. Rämemännikön juuriston rakenne ja kuivatuksen vaikutus siihen. Referat: Der Wurzelaufbau der Kieferbestände auf Reisermoorböden und seine Beeinflussung durch die Entwässerung. Acta Forest. Fenn. 65. 3.

—»— PÄIVÄNEN, J. and SARASTO, J. 1964. Groundwater table and water content in peat soil. Acta Forest. Fenn. 77. 1.

—»— and SEPPÄLÄ, K. 1963. Kuivatuksen tehokkuus ja turpeen lämpötalous. Summary: The effect of drainage degree on temperature conditions of peat. Acta Forest. Fenn. 76. 4.

HINTIKKA, V. 1964. Psychrophilic basidiomycetes decomposing forest litter under winter conditions. Comm. Inst. Forest. Fenn. 59. 2.

HUIKARI, O. 1953. Tutkimuksia ojituksen ja tuhkalannoituksen vaikutuksesta eräiden soiden pieneliöstöön. Summary: Studies on the effect of drainage and ash fertilization upon the microbes of some swamps.

—»— 1954. Experiments on the effect of anaerobic media upon birch, pine and spruce seedlings. Comm. Inst. Forest. Fenn. 42. 5.

ISOTALO, A. 1951. Studies on the ecology and physiology of cellulose-decomposing bacteria in raised bogs. Acta Agralia Fennica 74.

KOEPF, H. 1953. Die Verwendung des Ultrarotabsorptionsschreibers (URAS) für die Kontinuierliche Registrierung der Bodenatmung im Freiland. Landwirtschaftliche Forschung. Bd. 5: 54—62.

LUNDEGÅRDH, H. 1924. Der Kreislaufe der Kohlensäure in der Natur. Jena.

LÄHDE, E. 1966. Kokeita selluloosan hajaantumisnopeudesta erilaisissa metsiköissä. Summary: Experiments on the decomposition rate of cellulose in different stands. Silva Fenn. 119. 1.

MEYER, F. H. 1959. Untersuchungen über die Aktivität der Mikroorganismen im Mull, Moder und Rohhumus. Arch. Mikrobiol. 33: 149—169.

—»— 1960. Vergleich des mikrobiellen Abbaus von Fichten- und Buchenstreu auf verschiedenen Bodentypen. Arch. Mikrobiol. 35: 340—360.

MULTAMÄKI, S. E. 1952. Suo metsän kasvupaikkana. Summary: Swamps as a habitat for forests. Comm. Inst. Forest. Fenn. 40. 27.

PAARLAHTI, K. 1961. Tutkimuksia eräiden luonnontilaisten ja metsäojitettujen soiden pieneliöstöstä ja niiden ympäristötekijöistä. Unpublished. Department of Peatland Forestry. University of Helsinki.

—»— 1964. Havaintoja pohjaveden korkeuden vaikutuksesta selluloosan hajaantumiseen rämeen ja korven turpeessa. Unpublished. Department of Silviculture. University of Helsinki.

RICHARD, F. 1945. Der biologische Abbau von Zellulose- und Eiweiss-Testschnüren im Boden von Wald- und Rasengesellschaften. Mitteilungen der Schweizerischen Anst. forstl. Versuchsw. Bd. 24: 297—397.

ROMELL, L. G. 1922. Luftväxlingen i marken som ekologisk faktor. Medd. Stat. Skogsförsöksanst. 19: 125—360.

—»— 1932. Mull and duff as biotic equilibria. Soil Sci. 34: 161—188.

ROVIRA, A. D. 1953. Use of the Warburg apparatus in soil metabolism studies. Nature (Lond.) 172: 29—30.

SIRÉN, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. Acta Forest. Fenn. 62. 4.

TRIBE, H. T. 1957. Ecology of micro-organisms in soils as observed during their development upon buried cellulose film. Microbial Ecology. Seventh Symposium Soc. gen. Microbiol. 287—298.

UMBREIT, W. W., BURRIS, R. H. and STAUFFER, Y. F. 1951. Manometric Techniques and Tissue Metabolism. Minneapolis.

VIRO, P. J. 1955. Investigations on forest litter. Comm. Inst. Forest. Fenn. 45. 6.

WAKSMAN, S. A. and PURVIS, E. R. 1932. The microbiological population of peat. Soil Sci. 34: 95—109.