STUDIES ON CONNECTICUT LAKE SEDIMENTS

II. CHEMICAL ANALYSES OF A CORE FROM LINSLEY POND, NORTH BRANFORD.

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ABSTRACT. Chemical analyses of samples from thirteen levels of a profile taken in the sediments below the deep water of a small eutrophic lake are recorded. Considerable increase in the inorganic content in the most recent unconsolidated sediment at the top of the profile, as compared with the levels immediately below, is taken to indicate recent erosion of cultural origin. The consolidated sediment has an approximately constant ash content down to 30 feet below the mud surface, near the bottom of the profile the ash rises rapidly. The silica content of the ash is essentially constant, the alumina is fairly constant except at the bottom of the profile where the sediment is rich in clay and correspondingly high in alumina. Iron, calcium, and particularly manganese, show complex distributions that are probably determined biochemically. The proximate composition of the organic matter present is essentially constant throughout the profile except in the modern unconsolidated mud. Diagenetic loss of organic matter is therefore believed to be strictly limited to the time during which the consolidated sediment is being formed. The distribution of organic matter in the profile is believed to indicate a rapid change from oligotrophy to eutrophy, followed by a long period of approximate equilibrium in a eutrophic condition. Making certain limiting assumptions, it is shown that the growth-curve of the whole biocoenosis of the lake qualitatively resembles that of a single individual or of a homogeneous population. It is suggested that such a mode of development is characteristic of biocoenoses in general. The nature of the trophic equilibrium is examined in relation to the nitrogen and phosphorus content of the mud; it is suggested that the rôle of benthic animals in releasing these nutrients into the lake is significant.

INTRODUCTION.

THE present paper is based on a study of the longest profile (L 10.) obtained by Dr. E. S. Deevey in the deposits below Linsley Pond, North Branford; the locality and general nature of this and other profiles have been discussed by Doctor Deevey (1939) in the first paper of the present series. Our very best thanks are due to Doctor Deevey for permitting us to use so large a part of the samples representing critical levels in the profile. Though the present study is based on the

Am. Jour. Sc.—Vol. 238, No. 7, July, 1940.
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stratigraphy below a single point in the lake, there is reason to believe that the results are typical of the sediments of the deeper part of the basin.

TECHNIQUE.

The material when received had been stored without preservative for some months in glass vials very little larger than the portions of the core; little indications of oxidative changes were visible on the surface of the material but care was taken in isolating material for analysis to remove the outer part of the core. The samples used in analysis were dried at 110° C. and determinations have been made in the following way:

Iron, colorimetrically, by α–α' dipyridyl (Hill 1930).

Aluminum, by difference after determining iron and the weight of the ammonia precipitate.

Phosphate, using wet oxidation with concentrated hydrogen peroxide (Ohle 1938).

Titanium, colorimetrically with thymol in concentrated sulphuric acid.

Magnesium, using Kolthoff's titan yellow method (Barnes 1928) all samples and standards being adjusted to constant calcium content, except in the case of the 40 foot sample, where the magnesium was highest and where the usual gravimetric method was used.

All other inorganic determinations were made according to the procedure given by Hillebrand and Lundell (1929).

Lignin was determined as recommended by Steiner and Meloche (1935). By *apparent lignin* is meant organic material insoluble in cold concentrated (72%) sulphuric acid, *true lignin* is obtained by subtracting the protein equivalent of the nitrogen in the apparent lignin.

Total nitrogen was determined by the ordinary Kjeldahl method.

Some determinations of hemicellulose, after hydrolysis with dilute hydrochloric acid were made, but it was found difficult to obtain consistent results and the figures cannot be regarded as satisfactory. In the course of these attempted determinations of hemicellulose, the residue after hydrolysis in 2 per cent HCl., was collected and weighed. An aliquot was ashed, and from the loss in weight on hydrolysis, and the difference in ash content of the hydrolysed and unhydrolysed sample, the *loss on hydrolysis* in dilute acid could be computed. This includes hemicelluloses and doubtless the less stable protein material. The number of determinations by difference renders the results for the lowest part of the profile uncertain.

GENERAL NATURE OF THE SEDIMENTS.

Analyses were made on samples from the surface of the unconsolidated mud, corresponding to the sludge of Twenhofel's papers, in the vicinity of Doctor Deevey's L 10 boring, and from twelve levels in the latter. The lowest two samples (40 and 43 ft.) consist of a silty clay; this clay is presumably underlain by glacial sand. Above 40 feet the organic content increases, giving above 36 feet a typical autochthonous organic-rich sediment characterised by Deevey (1939) as coarse-detritus ooze. The unconsolidated sediment, though much poorer in organic matter than the consolidated samples between three and 36 feet, appears macroscopically in a wet state as a typical organic mud. Microscopic examination to be reported in greater detail by Deevey, does not permit distinction to be made between planktogenic and other kinds of organic detritus.

Total Ash. The total ash content of the sediments is very uniform throughout the consolidated coarse-detritus ooze from three to 34 feet below the lake bottom; in the deeper part of the section there is a marked increase in ash. The unconsolidated mud, forming the modern lake bottom, is, however, very much richer in unignitable material than the consolidated ooze on which it rests. Ash determinations of other samples taken from different parts of the basin have all given comparable figures, so that it seems certain that the sediment now being deposited is richer in inorganic material than the sediment deposited in the period reaching from the immediate past (three foot sample) back to at least the middle of post-glacial time (30 foot sample). Two possibilities must be considered in explaining this phenomenon. Either in the immediate past the lake was more productive than at present, or the quantity of silt brought into the basin has markedly increased in recent times. At the present time Linsley Pond is more productive of phytoplankton than any of about thirty other thermally stratified lakes investigated in Connecticut. It is therefore inherently improbable that during the second half of post-glacial time, down almost to today, it could have been so much more productive as to have deposited two and a half times as much organic sediment per unit mass of inorganic material as is produced in the lake at the present time. It is in fact inherently probable that the organic matter deposited in unit time has increased, as it is generally admitted by limnologists

Table I.

Inorganic Constituents.

Depth in feet	Loss on ignition	% of total sample (dried at 110° C.) SiO$_2$	Fe_2O_3	Al_2O_3	TiO_2	P_2O_5	MnO	CaO	MgO	SO_3	Summation of %*	Dry Weight of ice of wet mud in grms.	% of ash SiO$_2$	Fe_2O_3	Al_2O_3	TiO_2	P_2O_5	MnO	CaO	MgO	SO_3
0	28.8	47.3	12.1	5.5	0.08	0.254	0.23	1.2	1.0	1.0	97.5	.1261	66.5	14.3	10.3	0.12	0.357	0.37	1.7	1.4	1.4
3	51.9	34.4	6.4	3.6	0.08	0.117	0.12	1.1	0.3	2.1	100.1	.1232	71.5	13.3	7.4	0.24	0.242	0.24	2.3	0.6	4.5
8	54.0	33.0	4.8	3.8	0.10	0.133	0.11	1.4	0.3	1.0	98.6	.1245	71.8	10.2	8.4	0.22	0.289	0.25	3.0	0.64	2.1
13	49.8	35.8	6.2	3.9	0.07	0.135	0.09	1.1	0.61	1.5	99.2	1218	71.4	12.3	7.7	0.17	0.269	0.18	2.2	1.27	3.0
18	49.5	37.8	4.3	4.1	0.09	0.140	0.10	1.2	0.51	1.3	99.1	.1398	74.8	8.4	8.3	0.23	0.277	0.20	2.4	1.1	2.4
24	54.2	35.9	3.1	3.2	0.06	0.110	0.08	1.2	0.27	1.8	99.9	.1229	78.5	6.7	7.0	0.14	0.240	0.16	2.6	0.59	3.9
26	55.2	30.4	3.9	5.0	0.08	0.149	0.15	1.5	0.34	2.1	98.8	.1234	68.0	8.7	11.3	0.18	0.333	0.33	3.2	0.77	4.7
30	59.0	28.6	4.5	3.3	0.05	0.108	0.09	1.3	0.71	1.7	99.4	.1198	69.6	10.9	8.2	0.12	0.263	0.26	3.2	1.73	4.0
34	46.0	37.0	7.8	4.1	0.18	0.096	0.11	1.0	0.68	1.9	98.9	.1320	68.5	14.3	7.7	0.33	0.178	0.20	1.84	1.3	3.6
36	28.7	50.0	9.3	6.2	0.25	0.087	0.30	2.1	0.62	1.9	99.5	.1867	70.0	13.0	8.6	0.35	0.122	0.41	3.0	0.87	2.7
38	23.8	50.2	9.3	8.4	0.25	0.055	0.55	2.7	0.48	3.2	99.0	.2750	66.0	12.2	11.0	0.33	0.072	0.72	3.5	0.63	4.2
40	7.4	63.6	9.2	10.3	0.63	0.078	1.03	1.9	1.77	2.1	98.0	.6735	68.6	10.0	11.0	0.69	0.084	1.11	2.1	1.91	2.3
43	2.9	73.0	4.3	15.0	0.71	0.105	0.11	1.2	1.2	0.44	99.0	.7692	75.1	4.4	15.5	0.73	0.108	0.11	1.23	1.25	0.46

* Losses indicated by the figures in this column probably indicate failure to precipitate all the SiO_2 present. No detectible amounts of sodium, potassium or chlorine were found in the bottom two samples.

that cultivation of a lake basin tends to increase productivity. In the Linsley basin there is moreover no sign of any past or present human activity that could account for a marked decrease in productivity, so that the hypothesis of reduced organic sedimentation is a very improbable one. On the other hand, the difference in the ash content of the unconsolidated mud and the ooze immediately below it, is easily explained as the result of increased erosion following partial clearing and cultivation of the basin, which has been in progress at least since the eighteenth century. If it be assumed that the organic production in the lake has remained constant between the period of the three foot level and the present time, and that no appreciable fraction of organic matter is lost diagenetically in forming the consolidated mud, the difference in the ash content of the surface mud and the three foot sample indicates a rate of silting at present 2.6 times that occurring at the time the three foot deposit was formed. Actually both assumptions probably err in giving too low a figure. This large deduced increase is striking in spite of the fact that in Connecticut soil erosion is a much less pressing problem than in many parts of North America. Twenhofel (1938) reports a similar increase in the silica content of the recent mud (sludge) compared with the consolidated mud of Lake Monona, Wisconsin, and attributes this to human agency also. Owing to the inherent probability that the high ash-content of the modern mud is of artificial origin, the unconsolidated top of the core must be omitted in discussion of natural changes in productivity.

Silica. In general the distribution of silica in the profile follows that of the ash, of which it forms 66.0 to 78.5 per cent. In eight out of 13 levels the silica content of the ash lies between 68 and 72 per cent. Such variations as are shown may be due partly to diatoms contained in the sediments, but they are clearly of no great significance. The absence of any general trend suggests that the silt brought into the lake has a rather constant silica content.

Alumina. Throughout the greater part of the profile, from the surface to 36 feet, the alumina content of the ash is also essentially constant, being in general nine per cent of the ash. The high value at 26 feet, however, should be noted. The silty clay at the bottom of the profile has a markedly higher alumina content, as indeed is to be expected.

Iron. Iron, determined as Fe_2O_3, is doubtless entirely in the ferrous state in the original mud; much of it is certainly present as sulphide (hydrotroilite) but the amount of sulphate present after ignition suggests that a considerable part of iron must be present in some other form. The iron content of the sediments shows fairly marked variations. Calculated in terms of the ash, the iron content exhibits a well-defined maximum at 34 feet, a minimum at 24 feet, and an irregular upward trend to a second maximum in the unconsolidated mud.

Manganese. Unlike the previously discussed constituents of the ash, the manganese content exhibits a very marked maximum, apparent whether computation be made on the basis of dry weight or ash weight, at 40 feet, declining to an essentially constant value above 34 feet.

Titanium. The very small amounts present appear to show a steady decrease from the bottom of the profile upwards to about 30 feet, above which level only irregular variations have taken place.

Calcium. Three maxima in calcium depositions are to be noted. The first and best defined maximum is at 38 feet. The two secondary and perhaps not significant maxima correspond to periods of maximum organic content and may represent biological precipitation of calcium. Carbonate has not been determined and is included in the ignition loss. It is certainly low.

Magnesium. This element is present in relatively small amounts. There is a feebly indicated maximum at 40 feet but on the whole the quantity present decreases from the bottom of the profile upwards, though the modern unconsolidated mud appears to be abnormally rich in the element.

Sulphate. The sulphate of the ash presumably represents sulphide in the original sediment. The vertical distribution is essentially like that of calcium, but as some loss is possible on ignition, no great reliance can be placed on the variations. There is certainly not enough of the element present to form ferrous sulphide with all the iron present.

Phosphate. The total phosphorus, determined as phosphate after wet oxidation, is very low, at most levels about 0.06 per cent (as P or 0.1% P_2O_5) of the dry weight. The vertical distribution suggests that early in the history of the lake phosphorus entered in the form of an easily eroded mineral, declining in quantity with aluminum. Later, from 38 feet upwards, the phosphorus increases with the total nitrogen and is probably largely of organic origin. The biochemical importance of this element is discussed in greater detail below.

DISCUSSION OF INORGANIC CONSTITUENTS.

The general constancy of the silica content of the ash suggests that this substance may be used as an acceptable standard against which the variations of the other elements present can be assessed. The distributions of the principal inorganic constituents, per 100 parts of silica, are shown graphically in Fig. 1. In interpreting such a presentation, it is important to realise that the quantity of any material laid down in unit time in the sediment may be determined by events both inside and outside the lake. There can be very little doubt that the high alumina content at the bottom of the profile is due to easy erosion of alumina-rich material in the basin in early post-glacial time leading to the deposition of clay at the bottom of the profile. It would be difficult, however, to account for curious cyclical deposition of iron apparently indicated in the curve for that element, or for the very marked maximum in the manganese curve, by any such events outside the lake. Both the iron and manganese curves therefore probably reflect biochemical changes in the lake itself; unfortunately at the moment not enough is known of the cycles of these elements to suggest the underlying causes of the observed distributions. It is perhaps worth mentioning that, although in both north-eastern Wisconsin and in north Germany, as in Connecticut lakes, including Linsley Pond, and elsewhere, the waters of the hypolimnia of the majority of lakes contain considerably more iron than manganese; in a few lakes, for instance Trout Lake (Juday, Birge and Meloche 1938) and Grosser Plöner See (Ohle 1934) manganese is present in greater concentration than is iron. No geological reasons for these exceptional cases have been given and it seems more probable that an explanation must be sought in the chemistry of the lake itself. It is not impossible that the existence of a high manganese period in the sedimentary history of a lake, and of particular lakes with high manganese concentrations in the hypolimnion may be interrelated.

An interesting situation is found in the case of calcium, which shows a definite maximum at 38 feet and two less well defined

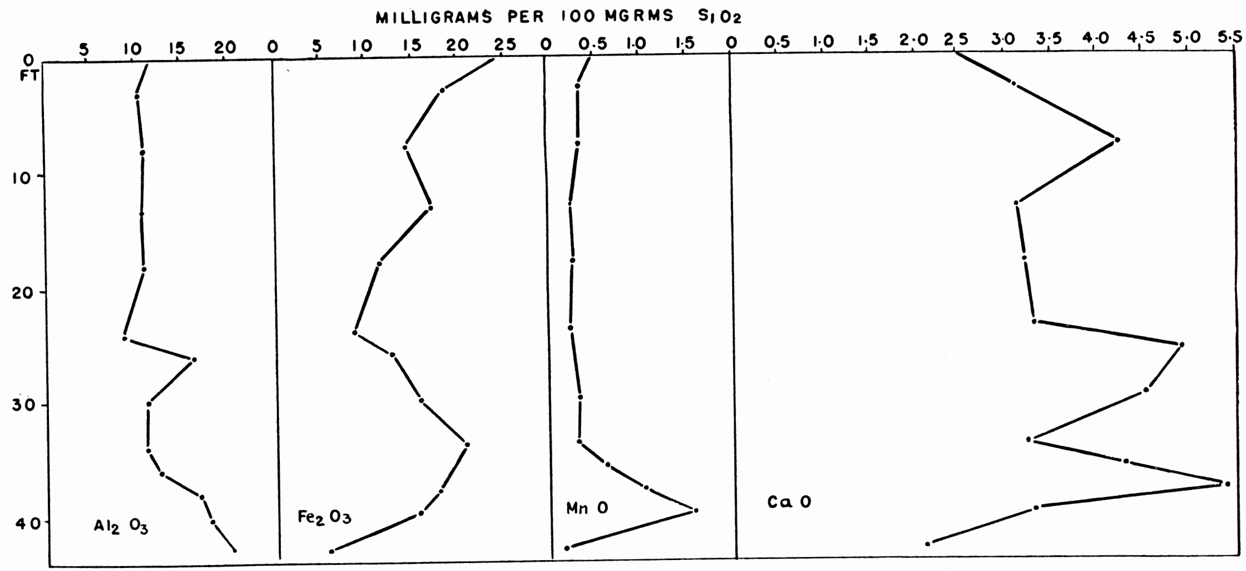

Fig. 1. Vertical distribution of aluminum as Al_2O_3, iron as Fe_2O_3, manganese as MnO, and calcium as CaO per 100 parts of SiO_2.

later maxima. The total amount of the element present at any level is, however, small. Many European lakes show a very marked period in their history characterised by deposition of calcium carbonate (e.g. Gr. Plöner See); this calcareous phase is often attributed to climatic amelioration after the retreat of the ice, though it does not always fall in the same climatic period (Tidelski 1929, Groschopf 1936). It is therefore noteworthy that the major maximum of calcium in the sediments of the Linsley Pond profile, corresponds in time to the boundary between Deevey's periods A1 and A2, when the spruce forest was at a maximum. Deevey has given good reason for believing that the spruce maximum represents the culmination of a cold period at the time of a local readvance of the ice-border.

The variations of the other inorganic constituents are so small or so irregular as not to warrant further discussion.

In considering the organic constituents, the first important problem is to decide whether the very great difference between the lower and the upper parts of the profile represents a progressive change in the characters of the sediment laid down, which may have become richer in organic materials as time progressed, or whether diagenesis has continued in the older deposits after they have been covered by more modern sediments, leading to a loss of organic matter from the lower part of the profile. In the case of Lake Mendota, Twenhofel (1933) believes that the latter hypothesis is correct, though in later work on Crystal Lake, Wisconsin, Twenhofel and Broughton (1939) consider that a real variation in the organic content of the sediments laid down has taken place. In the present case we incline strongly to the view that the organic content of the sediments at all levels, save the unconsolidated surface mud, bears essentially the same relation to the original organic material deposited at the bottom of the lake, and that diagenetic changes are chemically significant only in the formation of consolidated ooze.

Although little is known of the true chemical nature of the organic materials commonly classed as lignin and crude protein[1] that compose three-quarters of the ignitable part of the Linsley

[1] An experiment in which air-dried mud from 26 feet was treated with 1 cc. of one per cent pepsin (Merck) in 2 cc. of distilled water and 3 cc. of 0.5 per cent HCl for 48 hours at 37 C. gave negative results (to within one per cent) for protein loss by peptic digestion.

Table II.
Organic Constituents.

Depth in feet	% of total sample (dried at 110° C.)							% of ignition loss				mgrms per 100 mgrms of ash		
	Loss on Ignition	Total crude protein	Apparent lignin	"Protein" in lignin	True lignin	Non-ligneous protein	Organic loss on hydrolysis on 2% HCl	Total crude protein	Apparent lignin	True lignin	Organic loss on hydrolysis	Total crude protein	Apparent lignin	True lignin
0	28.8	8.8	13.2	2.7	10.5	6.1	14.8	30.5	45.8	36.5	51.3	12.4	18.5	14.7
3	51.9	14.0	30.8	6.6	24.2	7.4	18.1	27.0	59.3	46.5	34.9	29.1	64.0	50.3
8	54.0	13.3	35.2	7.3	27.9	6.0	14.7	24.6	65.2	51.7	27.2	28.9	76.6	60.7
13	49.8	13.7	31.6	5.9	25.7	7.8	16.1	27.6	63.4	51.6	32.3	27.3	62.9	51.2
18	49.5	13.8	29.4	6.7	22.7	7.1	18.1	27.9	59.4	45.9	36.6	27.3	58.2	45.0
24	54.2	13.0	29.8	5.5	24.3	7.5	21.3	24.0	54.8	44.8	39.3	28.4	65.0	53.0
26	55.2	16.4	31.2	8.4	22.8	8.0		29.7	56.5	40.7		36.6	69.7	50.9
30	59.0	13.1	37.4	8.1	29.3	5.0	19.9	22.2	63.4	49.7	33.7	32.0	91.2	71.5
34	46.0	12.6	30.4	8.4	22.0	4.2	16.6	27.4	66.1	47.8	36.1	23.3	56.3	40.7
36	28.7	7.9	17.0	4.2	12.8	3.7	10.6	27.5	59.2	44.6	36.9	11.1	23.8	18.0
38	23.8	6.8	15.3	2.9	12.4	3.9	9.1	29.1	64.2	52.7	38.2	8.9	20.1	16.3
40	7.4	2.1	3.8	0.85	2.95	1.25	(3.4)	28.4	51.3	39.4	46.0	2.3	4.1	3.2
43	2.9	0.54	1.4	0.3	1.1	0.24	(1.1)	18.6	48.3	37.9	37.9	0.56	1.4	1.1

sediments, it is safely assumed that the lignin is the most resistant of all the organic substances present. It would therefore be expected that if diagenetic changes had continued long after the deposition, the ratio of lignin to total ignition loss would tend to increase in progressively deeper sediments. Inversely, since the nitrogen not associated with lignin is probably contained in one of the least resistant fractions of the organic matter, the crude protein (N x 6.25) content of the ignition loss should decrease with increasing age if extensive diagenesis had occurred. Actually if the mean lignin or mean crude protein as percentages of the ignition loss for the column between three and 26 feet, where the organic content is approximately constant, be compared with the corresponding means for the column between 30 and 40 feet, where the organic content is falling, it will be seen that there is no evidence of a change in the proximate composition of the organic matter present.

	Lignin ("true")	Crude protein
Mean 3-26 ft.	46.9	26.7
Mean 30-40 ft.	46.9	26.9

A comparable result is obtained if the mean organic matter hydrolised in dilute acid is considered. This, like some of the nitrogen, must be regarded as an easily lost fraction. The amount of the loss is too small to be obtained accurately for 40 and 43 feet, but considering the other consolidated levels we find

Mean 3-24 ft.	34.1
30-38	36.2

In passing up from the consolidated to the unconsolidated mud, however, it will be observed that the organic matter of the latter is poorer in lignin (36.5 per cent) and slightly richer in crude protein (30.5 per cent) than are any other individual samples. The easily hydrolysable fraction of the organic matter is also much increased (51.4 per cent). It is therefore probable that some diagenetic change in organic constituents occurs in the formation of the consolidated ooze from the loose mud in contact with water, but that once the ooze has been consolidated, little change occurs. The Linsley data, however, do not show so great a change in the ratio of lignin to organic matter in passing from the unconsolidated to the consolidated deposits, as is indicated in Twenhofel and Broughton's Crystal Lake data (Lignin to ignition loss 1 : 15 - 16 in unconsolidated, 1 : 3 in consolidated deposits).

Origin of Organic Sediment. Microscopically most of the organic sediment consists of a pale brown coarse detritus, and it is not possible to distinguish material produced in the lake from that derived from trees growing in the basin. The greatest increase in organic matter (Fig. 2) in the sediments took

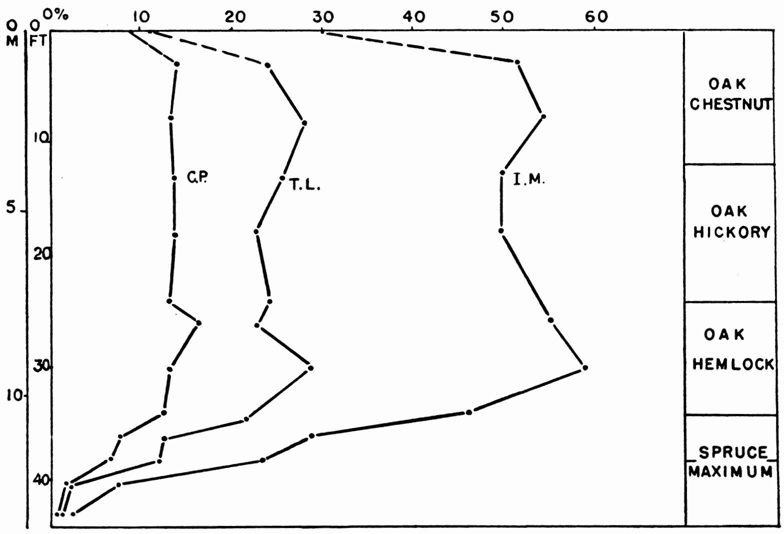

Fig. 2. Percentage content of crude protein (C.P.), true lignin (T.L.), and ignitable material in dried mud, plotted against depth. The major vegetation periods based on Deevey's pollen analyses are given at the right of the diagram.

place during the rise and fall of the spruce forest in the periods A1 and A2 of Deevey's chronology, and was apparently unaffected by the changes in the vegetation in the early history of the basin. It is therefore reasonable to conclude that the greater part of the organic matter in the sediments was derived from planktonic and other organisms living in the lake.

Climatic Significance. If, as seems probable, the spruce maximum at A1 - A2 represents a post-glacial cold period, it is clear that the climatic changes taking place in the early history of the basin have not significantly impeded the steady rise in the organic content of the sediments.

TYPOLOGICAL INTERPRETATION.

Since neither changing climate nor changing vegetation in the drainage basin appears to be responsible for the difference in organic content at the different levels of the profile, it appears probable that the variation observed is due to the relative amounts of silt brought into the lake and of organic matter formed therein. In order to investigate the very important corollaries to this conclusion, it is necessary to discuss the possibility of setting limits within which a relative time scale must lie.

Construction of a time scale.

It is probable that early in the post-glacial history of the lake, erosion was more rapid in the basin than to-day. If this were actually the case, the inorganic sediments laid down at the bottom of the profile were deposited more rapidly than the inorganic matter of the upper consolidated mud. It is, however, improbable that at any time unit thickness of sediment was deposited more rapidly than during the period of high organic deposition. Since a unit volume of sediment at the bottom of the column contains about ten times as much ash as a unit volume between three and 30 feet, deposition at such a rate that the volume of sediment deposited were constant, would allow ten times as much erosion in the basin in immediate post-glacial times as occurred in the latter half of the period under consideration prior to European settlement. This assumption, of unit volume in unit time, is referred to below as assumption 1. It seems probable that such an assumption grossly over-emphasises the erosion at the beginning of the history of the profile, for pollen analysis indicates that there was already a well-developed forest cover present. As a second limiting assumption (assumption 2) we suppose that inorganic sedimentation has been approximately constant, unit mass of ash being deposited in unit time. This is rendered improbable by the high alumina content at the bottom of the profile, and the true condition probably lies in between the limits set by these assumptions. In Fig. 3 the mass of ignitable matter, lignin and crude protein per unit wet volume are plotted against depth. If assumption 1 is correct, such curves may be regarded as representing growth curves of the biocoenosis of the lake, for since diagenetic change is limited to the mud-water interface, the organic matter deposited may be reasonably regarded as a relative measure of the organic matter produced. The corresponding curves based on assumption 2 must be prepared by more elaborate treatment. It is necessary to arrange the depths at which observations were made, on a scale graduated so that one unit on the scale corresponds to unit deposition of ash. This is done by plotting the ash content per unit wet volume against depth and integrating between the bottom and each depth planimetrically. The depths are then

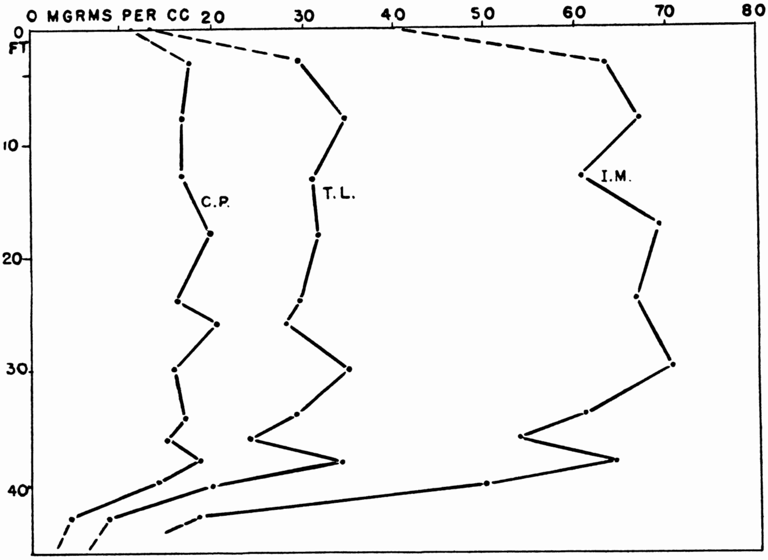

Fig. 3. Crude protein (C.P.), true lignin (T.L.) and ignitable material (I.M.) per cubic centimeter of wet mud plotted against depth. These curves give relative measures of organic deposition on the basis of assumption 1 (constant rate of sedimentation of unit thickness).

spaced from the bottom upwards at distances equal to the successive values of the integral. Using such a time scale, the three measures of organic matter must be expressed in parts per 100 parts of ash. This process has been carried out in Fig. 4.

The growth curve of a biocoenosis.

Considering now any of the methods of estimating organic matter and therefore of organic production, based on either of the time scales in Figs. 3 and 4, one very important char-

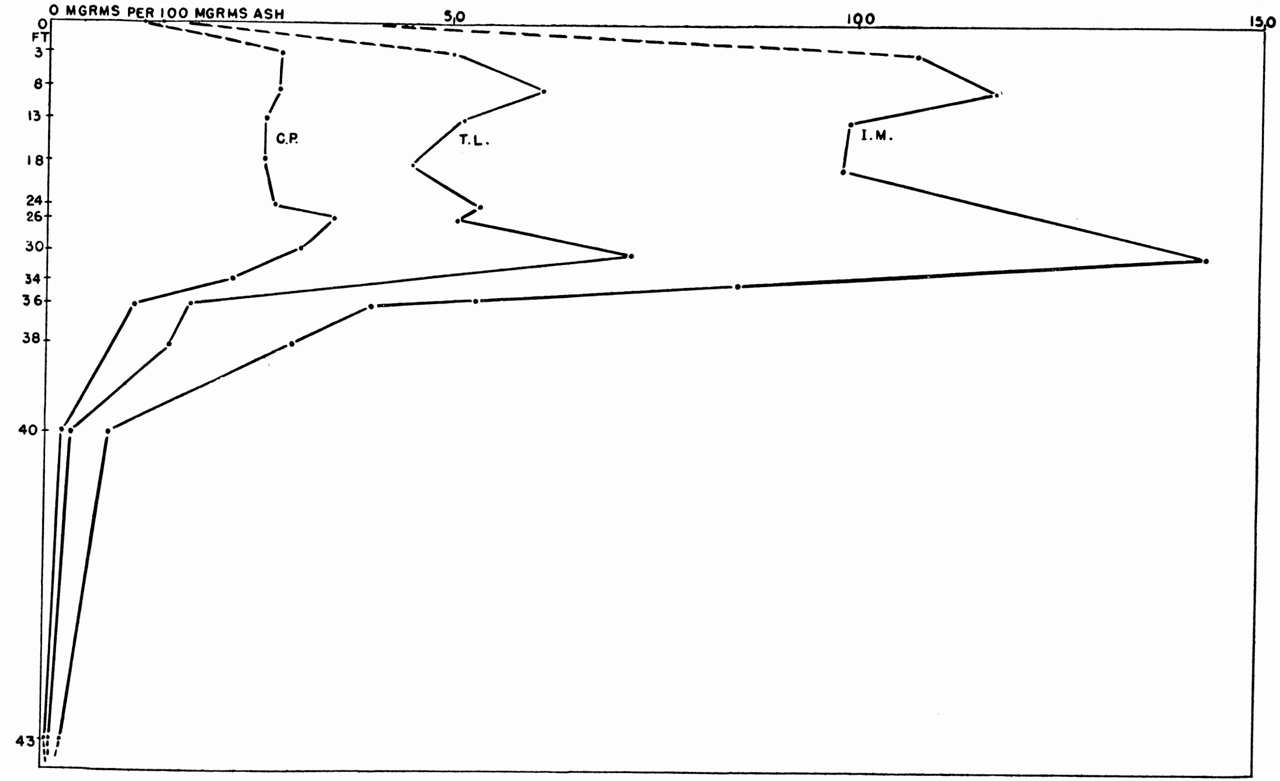

Fig. 4. Crude protein (C.P.), true lignin (T.L.), and ignitable material (I.M.) per 100 parts of ash, plotted against a scale proportional to the total ash deposited. These curves give relative measures of organic deposition on the basis of assumption 2 (constant rate of sedimentation of unit mass of ash).

acteristic will immediately be apparent. In every case there is an indication, not of a steady rise in productivity throughout the entire post-glacial history of the lake, but of a sudden rise followed by a long period in which the composition of the sediments shows but slight and irregular variations and which must therefore be regarded as a period of trophic equilibrium. According as to whether assumption 1 or assumption 2 is used in the construction of a time scale, this period of equilibrium extends from the top of the consolidated mud to 40 or 30 feet respectively. Certain minor variations in the equilibrium period are to be noted and are discussed below; on the whole, however, the constancy of the organic composition during the equilibrium period is most striking.[2] Moreover, on the basis of assumption 2, there is a prolonged period during which productivity is slowly rising before the great increase preceding equilibrium. The initial slow increase is not shown if assumption 1 is employed but as Deevey (1939) has pointed out, other shallower profiles indicate that there is probably a layer of sterile sand below the clay, which could not be reached by the borer at the base of profile L 10. It seems therefore very probable, on whatever hypothesis as to the time scale is adopted, that organic production in the lake at first occurred slowly, then with increasing rapidity, and finally after a maximum in the rate of increase, an equilibrium period intervened, so producing a sediment of relatively constant composition until the cultural disturbance of the present time. Certain observations on the quantitative micropalaeontology of the sediments, to be discussed by Doctor Deevey in a later communication, strongly suggest that assumption 2 is more nearly correct than assumption 1. Probably the true form of the curve relating organic deposition and time lies between that of Fig. 4 and that of Fig. 2, where simple percentages are plotted against depth. Mr. Preston Smith informs us that a comparative study of all available North American pollen profiles, in conjunction with other data, suggests a relatively long duration for the coniferous period (A of Deevey's scheme) and so favours assumption 2.

[2] If it be objected that assumption 1 still does not allow enough sedimentation of clay and silt per unit of time in immediate post-glacial times, it must be supposed that productivity has declined since the 40 foot level. Such knowledge as is available as to typological succession in lakes makes this objection a very improbable one.

It is impossible to avoid qualitative comparison of this mode of development of the rate of organic production of sediment, and so within certain limits[3] of development of the mass of organisms present, to the growth curves of individual organisms and homogeneous populations. In the cases of such systems, growth depends firstly on the tendency of cells or individuals, multiplying unrestrictedly, to increase the mass of the system geometrically, and secondly on the limitation to normal metabolism apparently set by the presence of a large aggregate of cells integrated to form a single organism, or by large numbers of individuals competing in a limited space. The interaction of these two tendencies produces the well-known logistic or sigmoid curve of growth. In view of the apparent if somewhat rough resemblance of the curve of development of the biocoenosis to such a sigmoid growth curve, it is well to examine whether there is any probability of such a type of curve representing the growth of a biocoenosis or, to use botanical nomenclature, the development of a sere. In considering such a possibility, it is necessary to emphasise the important distinction between the individual or homogeneous population, where all cells or individuals at any one time are in genetic continuity with a single ancestor or ancestral pair, and the developing biocoenosis or sere, where the individuals present at any time in the process of succession are by no means necessarily the descendants of the original colonists. In the cases where genetic continuity is present, it is obvious that there is a tendency to geometrical increase; in the case of a series of unrelated organisms successively inhabiting the same biotop, such a tendency is not immediately self-evident. However, considering the simplest and best studied case, the colonisation of a bare surface by pioneer plants, it is well known that the earliest colonists not merely play an essential part in preparing the ground for qualitatively different successors, but also, by soil-formation, nitrogen-fixation, etc., bequeath to these successors a substrate potentially capable of supporting a quantitatively greater flora. Such a process would produce an effect essentially similar to that of the tendency to geometrical increase in genetically continuous systems.

[3] Compare Riley's (in press) observations that indicate that when the plankton crop per unit area increases above a certain limit, it has little effect on productivity.

That little emphasis has been placed on this aspect of ecological succession, and that when it has been observed, as must often have been the case, it has been deemed trivial, is doubtless due to the bio-sociological bias of ecologists.

It is apparent that a very large number of scientific problems can be studied by two distinct methods. Following one method, the history of individual units and their interactions can be studied. This has been the underlying thought behind the bio-sociological part of ecology, in spite of the protests of synecologists that the community is an organism and is to be studied as a whole. That such a particulate bias has been introduced unconsciously is probably due to the obviousness of the individual units and the training of biologists in the taxonomic recognition of species. The association is therefore defined quantitatively in terms of relative numbers of different species. The equally important characteristic of the mass per unit area or volume has, at least in terrestrial ecology, been largely left either to the autecologist, studying fluctuations in natural populations of single species, or to the student of strictly applied ecology (e.g. agriculture), where problems of yield are economically significant and where the particulate approach is minimised by the homogeneity of the artificial associations considered.

The second method consists in the isolation of a suitable volume of space, either naturally (e.g. the whole earth, a lake) or arbitrarily (e.g. a cubic meter of sea-water or the living matter above a hectare of forest floor) defined, and then in studying the transference of matter and energy in a given time across the boundaries of this volume. Such a method is the starting point of thermodynamics and has been immensely powerful in the physical sciences. It is implicit in much of physiology and biochemistry, as in the study of tissue metabolism by means of respiratory quotients. In developing such an approach an estimate of the total quantity of living matter included in the volume under consideration, is of greater importance than an estimate of its taxonomic diversity. Ideally of course both methods should be used together; in practice, however, this is often impossible. As a result of the neglect of what may be called, using Vernadsky's term, the biogeochemical approach[4] some branches

[4] This mode of approach has long been recognised in limnology and as far as the difficulties inherent in moving water masses permit, in oceanography. A less rigorous, if simpler, statement of the two methods may be found in the introduction to Birge and Juday's (1911) monograph on the dissolved gases of the Wisconsin lakes (See also Thienemann, 1939).

of ecology, notably the study of succession, appear to have suffered. As an indication of the usefulness of results obtained by this approach in successional studies, it may be pointed out that the conclusions reached above, relating to the suddenness with which the biocoenosis developed in Linsley Pond, and to the prolonged period of equilibrium that followed this development, may well have a bearing on other cases where a highly carbonaceous sediment is found lying with a very narrow transition zone and without apparent unconformity, on less carbonaceous material.

Equilibrium typology and the climax formation.

The argument presented above indicates that in passing from an initial oligotrophic condition to a later eutrophic condition, Linsley Pond has reached an approximate equilibrium and that the change from one lake type to the other took place fairly rapidly. It is natural to enquire whether other observations exist that throw light on the generality of this type of succession. Although Doctor Deevey reached a similar conclusion from a qualitative study of the Chironomid microfossils in a less extensive profile, in Linsley Pond, and Lyd Hyt Pond nearby, as will be indicated in a subsequent paper of this series, neither Lyd Hyt Pond nor other Connecticut localities provide profiles of any value in elucidating the present question. In Lyd Hyt Pond the relationship of inorganic to organic sedimentation is obviously disturbed by a layer of silt interposed in what is presumably the equilibrium period, and probably due to some local catastrophic event increasing erosion in the basin for a short period of time. In all the other localities studied by Deevey, there is too great a probability of litoral vegetation influencing the upper part of the column to justify a study of the sort presented in the present paper. The only previous author who appears to have reached a similar conclusion as to the existence of a trophic equilibrium is Groschopf (1936) in his study of the sediments of the Grosser Plöner See. Groschopf's conclusion was based primarily on microscopic structure rather than on chemical analysis, but is evidently confirmed by the present investigation. In both Linsley Pond, and the Grösser Plöner See, the equilibrium is established at a relatively remote time, unfortunately only determinable on the pollen scale. It is therefore probable that the majority of lakes whose basins were formed as a result of glacial or pre-glacial events, have already reached trophic equilibrium.

In some respects the trophic equilibrium in a lake corresponds to the climax of plant ecologists; as has been pointed out both are probably reached in ways that are quantitatively comparable. There is, however, one important difference between the two concepts which should be mentioned. Since the establishment of the trophic equilibrium occurs when a maximum in the rate of organic production is reached, it implies that the lake will be filling up faster with organic matter than at the stage immediately preceding equilibrium. This means that during the equilibrium period the lake, through the internal activities of its biocoenosis, is continually approaching a condition when it ceases to be a lake. In the case of the climax forest the presence of a stable tree cover may actually preserve rather than destroy the form of the substrate, so that the climax is a more permanent concept than the trophic equilibrium, which indeed it may succeed. This obvious generalisation merely expresses the inevitable difference in the relationship of physiographic and ecological succession when a biotop with a primarily concave substrate is compared with one whose substrate is primarily convex. In the one case physiographic succession is aided in the destruction of the character of the biotop by ecological succession; in the other case it is inhibited. Clements and Shelford (1939) believe that very large lakes such as Baikal and the Great Lakes of North America, contain true climax associations. Small lakes in which organic sedimentation is important, are regarded by these authors as part of the terrestrial sere. It is, however, improbable that there is a true qualitative difference between the large and small lakes. In Linsley Pond there have probably been two changes in the deciduous forest association around the lake during the period of trophic equilibrium. If as seems probable the benthic fauna has remained essentially unchanged during all this time (Deevey unpublished) the lake has probably a good claim to be regarded as containing a climax association. This matter will be discussed by Doctor Deevey in a later paper.[5]

[5] In a recent conversation with Dr. V. E. Shelford, he expressed the view that the benthic communities of small eutrophic lakes might well represent climaxes.

Variations during the equilibrium period.

The smaller variations of ignition loss between 30 and 3 feet remain to be considered, for though they are small compared to the variations between 43 and 30 feet (2.4 - 59 per cent) they are not inconsiderable (45 – 59 per cent). Two possibilities suggest themselves. Productivity may have varied somewhat, or at least the fraction of the organic matter produced that was buried, may have varied. It is also possible that the amount of inorganic sediment entering the lake varied. The two small pieces of evidence available point in different directions. On the one hand, the intense local silt deposition in Lyd Hyt mentioned above, might correspond to a feebler increase in erosion in the Linsley Basin, giving the small ash maximum at 18 feet. Unfortunately local peculiarities of the Lyd Hyt pollen spectrum prevent stratigraphic recognition of the level, corresponding to the silt band, in the Linsley profile. Such evidence as is available, however, suggests correlating the Lyd Hyt silt band with a lower level, about 26 feet in Linsley. On the other hand, there is an indication of secondary maxima in the calcium curves at the time of maximum organic content. This possibly indicates biological precipitation of calcium, but the maxima may not be significant. The smaller variations in the organic curve must therefore be left unexplained.

Mechanisms of the rapid increase and of the establishment of equilibrium in productivity.

There is both statistical (Riley *in press*) and experimental (Hutchinson *in press*) evidence that the productivity of Linsley Pond, as is to be expected on general grounds, is largely limited by the available supply of phosphorus and nitrogen compounds in the water. Moreover, it has been shown that in the case of the former element, a very large part of the total mass entering planktonic organisms at any time is derived from the mud, and is returned to the latter by sedimentation of organic debris. The small amount of phosphorus that is lost permanently to the sediment is replaced by a small excess of the phosphorus entering over that leaving the lake. There is every reason to suppose that the same is true of nitrogen compounds, except that assimilable nitrogen is probably liberated less quickly from the organic detritus than is phosphorus, proportionally more nitrogen being buried in the sediment, and that this loss can be made up by nitrogen compounds in rain water, in the inlets and by bacterial and algal (De 1939, Hutchinson *in press*) nitrogen-fixation in the lake. The nitrogen and phosphorus compounds present in the mud therefore constitute a supply of nutrients that at least partially can become available to organisms in the lake. The *nutrient potential* of this supply could in theory be measured by an estimate of the rate of loss from unit area of mud in unit time. In practice the only possible measure of such a potential is based on the

TABLE III.

Depth	N mgrms. per cc. wet mud.	P mgrms. per cc. wet mud.	N/P
0	1.70	0.140	12.6
3	2.76	0.063	43.9
8	2.66	0.072	36.9
13	2.66	0.072	37.1
18	3.09	0.085	35.9
24	2.59	0.059	43.9
26	3.25	0.080	40.4
30	2.52	0.056	44.7
34	2.71	0.055	48.9
36	2.39	0.071	33.7
38	3.00	0.066	45.4
40	2.63	0.229	11.5
43	0.68	0.354	1.9

assumption that it will be proportional to the quantity of the element in question in combination in unit wet volume of mud. It is obvious that in expressing nutrient potential in past times in this way no allowance is made for compression of the lower part of the profile. We are, however, inclined to doubt that any very great error is introduced by neglecting compression, because in the upper part of the column, where the composition of the sediment is essentially constant, the dry weight of unit wet volume (Table I) is also essentially constant. In Table II the nutrient potential measured in this way is set out for both nitrogen and phosphorus, as is also the nitrogen-phosphorus ratio. The latter is found to fall very strikingly as the modern mud is approached; this is probably an expression of the greater ease with which phosphorus is regenerated, or from the standpoint of the sediment, lost diagenetically. The ratio in the modern, unconsolidated mud, is essentially the same as that in modern seston (three determinations, 1939, 9.4 - 25.5, mean 14.4). The high phosphorus content of the oldest mud is very probably largely due to inorganic sedimentation, and expressed in terms of percentage dry weight falls as the clay content falls. Later the phosphorus is probably largely sedimented as organic phosphorus. At the present time there is evidence that sedimentation of inorganic phosphate occurs only at the time of the autumnal overturn and that this phosphate has been derived during summer stagnation from the mud (Hutchinson *in press*). If assumption 1 can be accepted, unit thickness of sediment being deposited in unit time, it is clear that the development of the lake has been dependent on the development of a supply of combined nitrogen and that from 38 feet upwards the nitrogen and phosphorus supplies have been in harmony, producing after diagenesis a rather constant N/P ratio of about 40. Assumption 1, however, would seem to represent an extreme case, and if some time scale intermediate between assumptions 1 and 2 be adopted, we are faced with the difficulty that the lake increased in productivity over part of the time represented by the interval between the 38 and 30 foot samples, without a corresponding increase in nutrient potential, the nutrients being merely diluted by silt in the early part of the process, by water in the later part. Since some such intermediate time scale is inherently probable, this difficulty must be considered. There is moreover a very fundamental objection that can be raised against the concept of the phosphorus nutrient potential in general. The mud contains, as has been indicated, a large quantity of iron, which, except perhaps at the bottom, undoubtedly is in the ferrous state. Diffusion of phosphorus and iron in ionic form across the mud-water interface can only occur as phosphate and as ferrous ions and this will inevitably be followed by the oxidation of the iron and, at the pH encountered in Linsley Pond, by precipitation of the very insoluble ferric phosphate (cf. Einsele 1936). This difficulty is inherent in the whole theory of phosphorus regeneration from the mud, but as without this theory the major events in the lake are entirely incomprehensible, it seems reasonable to look for some process by which the effective diffusion of phosphorus from the mud can occur. The only possible mechanism seems to be the metabolic activities of benthic organisms, which may well be able to excrete phosphorus into the water independent of iron. The regulation of the metabolism of lakes by such animals as *Tubifex* has been stressed by Alsterberg (1924) and would seem to be the most likely way of resolving the dilemma. If this is in fact the explanation, it is easy to see that, even if the nutrient content per unit wet volume is constant, as the silt content of the sediment became lower and its water content higher, conditions for mud living organisms would improve, for to obtain unit quantity of food they would have to ingest less of the unnutritious inorganic constituents of the sediment. This in turn would lead to more rapid regeneration and greater organic production in the lake. The final equilibrium would probably be determined in all cases by the small balance of incoming nutrients in the inlet over the outgoing nutrients in the outlet. Since phosphorus is essential to nitrogen-fixing bacteria and algae as to other organisms, and all other biological elements are doubtless present in excess, it is probable that it is the phosphorus income that is the fundamental limiting factor. Further analysis of this and kindred questions cannot be undertaken until an absolute time scale can be constructed. Modern geochronological and geophysical methods suggest that the problem of such an absolute time scale, though difficult, is not insoluble.

Many ecologists have emphasised the dynamic aspects of successional changes; hitherto the dynamics involved have been almost purely qualitative and so hardly worthy of the name. There is obviously a large field of study awaiting exploration, as methods can be developed for the quantitative estimation of changes in biocoenoses over very long periods of time. It is hoped that the present contribution, in which only the first stage in a necessary series of successive approximations is attempted, represents at least a step towards a fuller exploration of this interesting and important realm.

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