Gunther Schlager, who furnished useful comments and criticism.

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ENERGY STORAGE AND THE BALANCE OF PRODUCERS AND DECOMPOSERS IN ECOLOGICAL SYSTEMS[1]

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INTRODUCTION

The net rate of change in energy or material stored in an ecological system or its parts equals the rate of income minus the rate of loss. These rates may be expressed for various trophic levels (Lindeman 1942) or species, and also for the accumulated dead organic matter. In forests, both the living and the dead materials accumulate substantial reservoirs of energy, as shown by caloric measurements of Ovington (1961), Ovington and Heitkamp (1960), and others.

The rates of loss from all reservoirs can be expressed conveniently by a parameter k, which equals the fraction of the stored quantity that is lost per (short) unit time, without implying yet whether these fractions are approximately constant or not. Jenny, Gessel, and Bingham (1949) and recently Greenland and Nye (1959) have used such fractional loss rates, as constants, in characterizing the turnover and build-up of dead organic litter and soil humus. A confusing difference in approach and formulas which these papers use can be resolved in the following review of simple mathematical models for litter production and de-
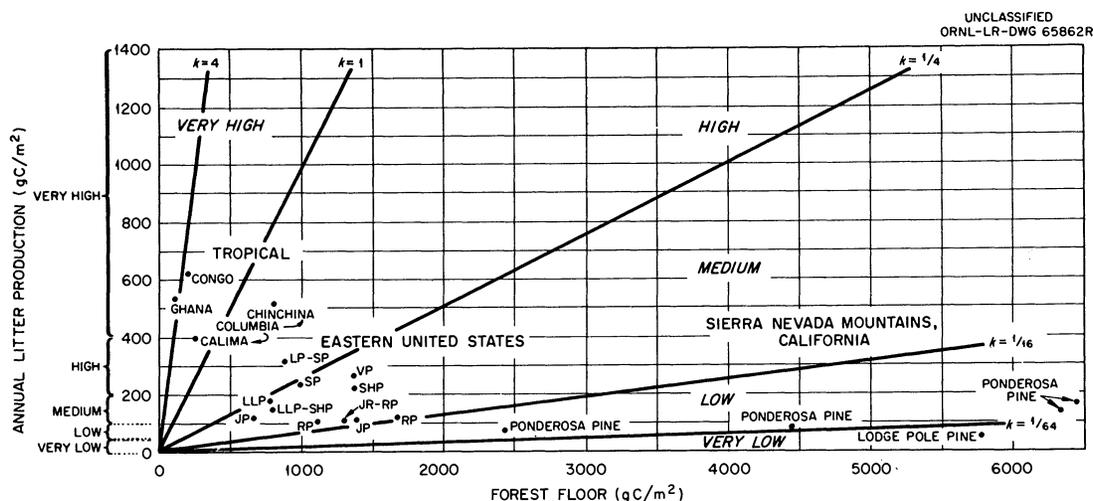
FIG. 1. Estimates of decomposition rate factor k for carbon in evergreen forests, from the ratio of annual litter production L to (approximately) steady-state accumulation of forest floor X_{ss}. Tropical data for Ghana from Nye (1961), for Congo from Laudelot and Meyer (1954), and for Columbia from Jenny (1950) for mixed forests at 30 m above sea level (Calima) and 1,630 m (Chinchina). Southern pine forest data adapted from Heyward and Barnette (1936) for *Pinus palustris* (longleaf pine, LLP), *Pinus elliotii* (slash pine, SHP) and mixtures on southeastern U. S. coastal plain; from Metz (1952, 1954) for *Pinus echinata* (shortleaf pine, SP) and its mixtures with *Pinus taeda* (Loblolly pine, LP) on the South Carolina piedmont; from McGinnis (1958) for *Pinus virginiana* (Virginia or scrub pine, VP) in the Appalachian Ridge and Valley province at Oak Ridge, Tennessee. Northern pine forest data from Minnesota adapted from Alway and Zon (1930) for *Pinus banksiana* (jack pine, JP), *Pinus resinosa* (red or Norway pine, RP) and mixtures. Sierra Nevada data from Jenny, Gessel, and Bingham (1949) and Jenny (1950) for *Pinus ponderosa* and *Pinus contorta* (lodgepole pine) at various elevations above sea level.

cay in idealized evergreen and deciduous forests. The wide range of decay rates estimated here from data on forests of very contrasting climates helps to account for the great differences in total accumulation of organic carbon on top of mineral soil (horizontal axis of Fig. 1), and in the promptness in approaching their maximum storage capacity for dead organic matter.

Ovington's examples (1961) confirm that a substantial fraction (often one-third to one-half or more) of the energy and carbon annually fixed in forests is contributed to the forest floor as litter fall (mostly leaves). Because of this, and because litter fall is generally related to the quantity of photosynthetic machinery in the system, it is an interesting index of ecosystem productivity. Fig. 1 shows a wide range in litter production, plotted along the vertical axis in terms of grams of carbon per square meter per year. Litter production is "very high," sometimes above 400 g/m² in tropical forests of America (Jenny et al. 1949) and Africa (Greenland and Nye 1959). It is "medium" or "high," 100-200 or 200-400 g/m², in the northern and southern pine forests of the eastern United States. California mountain forest data (Jenny et al. 1949), when expressed in terms of carbon (using C contents based on Jenny 1950) show medium to low production (50-200 g/m²).

"Very low" litter production, below 50 g/m² carbon, would normally indicate relatively nonproductive forest.

The scatter in any one portion of Fig. 1 indicates that the production and storage of dead organic carbon are not closely related. In fact, the diagram as a whole demonstrates an inverse relation. Low storage of carbon in the highly productive tropical forests contrasts with high levels of carbon and energy accumulation in the relatively unproductive cool temperate forests. A major reason for this inverse relation clearly involves rates at which dead organic matter is broken down or incorporated into the mineral soil by organisms. Chemical composition of coniferous litter, as well as low temperature, tends to retard biological activity in the northern or subalpine forests. Under the assumption that the forest floors in the stands here selected may approximate a steady state, one method of estimating the decay parameter k can be made from the ratio of the vertical and horizontal coordinates of each point on Fig. 1; other methods are also indicated below.

MODELS AND METHODS

Let X be measured either as ovendry weight, organic carbon, or energy in dead organic matter per square meter of ground surface, and let the

income rate, and either the amount or the fraction lost per unit time, be expressed in comparable units. The opening sentence on net rates of change for a discrete interval of time (day or year) Δt can be restated as:

$$\frac{\Delta X}{\Delta t} = \text{income for interval} - \text{loss for interval.}$$

$$(1)$$

For the model of steady income, L, the instantaneous rate of change is the limit as Δt and ΔX approach zero

$$\frac{dX}{dt} = L - kX \qquad (2)$$

The loss rate kX is considered as a product of the amount accumulated (X) and the instantaneous fractional loss rate, k, which will first be considered for the special case of a constant loss rate.

If and when accumulation reaches a steady-state level, X_{ss}, then (by definition of a steady state) the rate of change in equation (2) is 0, so income = loss.

$$L = kX_{\text{steady state}} = kX_{ss} \qquad (3)$$

For this case, the rate parameter k can be estimated by the ratio of income to steady-state total, as the ratio of the vertical axis over the horizontal axis of Fig. 1 (slopes of the diagonal lines).

$$k = L/X_{ss} \qquad (4)$$

While equation (4) represents one method of estimating loss rates from harvest of litter and forest floor materials in the field, experimental approaches are also being used for more direct estimates of loss rates (Shanks and Olson 1961, Olson and Crossley 1963). Where L and k can be estimated independently of X, then their ratio might be used to predict the steady-state level yet to be accumulated in an ecosystem which has not yet come to a balance of income and loss.

$$X_{ss} = L/k \qquad (5)$$

Decay with no production

The special case in which $L = 0$ approximates our current experiments (Shanks and Olson 1961) in which litter is confined in mesh bags and remeasured after loss of differential increments of material, dX. Equation (2) can be rearranged to express these losses as a fraction of the residue X currently remaining.

$$\frac{dX}{X} = - k \, dt \qquad (6)$$

The model for constant fractional weight loss implies (by integration) a constant negative slope,

$-k$, on a semi-log graph of the amount remaining from an initial quantity X_o at $t = 0$.

natural logarithm $(X) = - kt +$ natural
        logarithm (X_o) $\qquad (7)$

The fraction remaining is

$$\text{natural log } (\frac{X}{X_o}) = - kt \qquad (8)$$

Statistical estimation of this slope provides a second method for estimating the parameter k.

Taking antilogarithms of both sides of equation (8) gives the fraction remaining as a negative exponential function, like that shown on Fig. 2a.

$$\frac{X}{X_o} = e^{-kt} \qquad (9)$$

For example, after 1 year of biological decay and physical breakdown, the fraction remaining would ideally be $X/X_o = e^{-k}$. A third method for estimating the instantaneous rate of breakdown (really a special case of the second method) makes allowance for the change in weight loss, kX, which is due to changes in X (assuming k constant). Jenny expressed this loss as a fraction of the original total and called it k':

$$k' = \Delta X/X = 1 - X/X_o = 1 - e^{-kt} \qquad (10)$$

From equations (8) to (10), the relation of k' to the instantaneous decay rate k is:

$$k = - \text{ natural log } (X/X_o) = - 1n(1 - k') \qquad (11)$$

Where the time interval is short (e.g., expressed in loss per day), or where the decay is slow even for time units as long as a year, the change in X during the interval is small, k and k' are both small fractions of 1, and there is little numerical difference between them. However, for time spans as long as a year, the k' for litter decay is frequently a large fraction of 1, and k may be equal to 1 (as in Fig. 2) or may exceed 1 (see below). For $k = 1$, $k' = 1 - e^{-1} = 0.632$.

Accumulation with continuous litter fall (case 1)

For the case in which litter is almost steadily falling, at a rate L which the model assumes constant, equation (2) can be rewritten like equation (6) after dividing all terms by k:

$$\frac{dX}{(L/k - X)} = - k \, dt \qquad (12)$$

This has an integral like equation (7).

$$1n(L/k - X) = - kt - \text{constant} \qquad (13)$$

For an initial condition with no forest floor (e.g., burned off by ground fire), $X = 0$ at $t = 0$, and
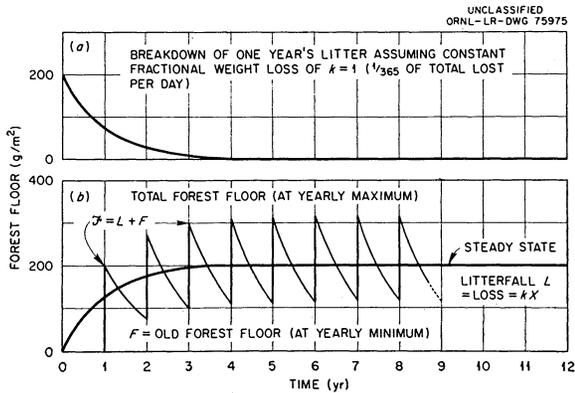
FIG. 2. a. Negative exponential curve for idealized litter decay, assuming weight loss proportional to amount remaining at any one time. b. Gradually rising exponential curve for accumulation under conditions of steady income and loss, compared with step-wise curve for additions and losses of litter in idealized deciduous ecosystem.

the constant in equation (13) is $-\ln(L/k)$. The antilog of equation (13) gives the solution—a rising curve like that shown in Fig. 2b.

$$X = (L/k)\,(1 - e^{-kt}) \qquad (14)$$

This curve is the mirror image of the curve for decay, shown in Fig. 2a, for the case $k = 1$ in yearly units, which is equivalent to a daily loss of 1/365 of the total weight remaining at any one time. As k increases or decreases, the steady-state level $X_{ss} = L/k$ decreases or increases accordingly. But there is also a speeding up or delay in the approach to this steady state, which is illustrated in Fig. 3 by the dashed lines (corresponding to solid lines for decay curves with the same value of k).

Accumulation with discrete annual litter fall (case 2)

Important differences between case 1, for steady fall, and case 2, for fall at the end of the growing season ("idealized deciduous forest") are illustrated by the jagged curve of Fig. 2b, for the same values of $L = 200\,g/m^2$ produced per year, and $k = 1$ (or 1/365 of total lost per day). There is no longer a steady replacement of the litter decomposing between pulses of litter fall, and the remainder of the 200 g after 1 year of decay ($e^{-1} = 0.368$) is less than the amount which had accumulated after either 1 or 2 years of steady fall and decay in case 1. This deficit below the theoretical level for steady accumulation is then made up by the second sudden "autumn" litter fall; but the more rapid loss, kX, again lowers X past the curve given for case 1. Because kX is higher in the first half of each annual decay cycle than in the second half, the steady state of the smooth

curve lies a little below the half-way level between the peaks and troughs for the discontinuous case. (Considering intermediate cases, e.g., with quarterly or weekly "installments" of litter fall, would still give a jagged curve with peaks and valleys straddling the rising curve of Fig. 2b, but with less amplitude between the extremes.)

An equation for the annual peak values $\mathcal{J}_n$ which occur right after the nth year's annual fall of litter differs from equation (14) only by the constant $L/k' = T$ for the theoretical limiting value (Olson 1959a, 1959b):

$$\mathcal{J}_n = (L/k')\,(1 - e^{-kn}) \qquad (15)$$

This is illustrated in Fig. 4, for the value of $k' = 0.25$ (so that $k = 0.288$ from equation (11)). Still lower values for k or k' of course would show slower decay and slower approach to the limiting value for accumulation. The values given are equivalent to the geometric series of Jenny et al. (1949) which developed directly from the annual increments of L (which they called A).

Between annual events of litter fall in the ideal deciduous model, decay is governed by equations (9) and (10). The value $\mathcal{J}_n$ is reduced to a value $F_n = (1 - k')\mathcal{J}_n$.

$$F_n = (L(1 - k')/k')\,(1 - e^{-kn}) \qquad (16)$$

When $\mathcal{J}$ approaches an upper limit of $T = 800$ g/m² in Fig. 4, F approaches an upper limit of $0.75T$ or $T - L$, namely 600 g/m².

After the limiting value T is approached, it is possible to estimate

$$k' = L/T \qquad (17)$$

which equals $A/(F + A)$ in Jenny's terminology, by analogy with equation (4). The ratio of equation (17) may thus be useful in characterizing decay where the deciduous model is a good approximation, and where autumn-peak values can be measured directly, or summed by taking late summer values (F) and adding the litter which falls in the autumn. Even in this case, it is necessary to use equation (11) if it is desired to find actual decay rates k, which can be converted to short time units simply by a change in time scale. In the case of a forest with little or no seasonal alternation, equation (4) can be used, as Greenland and Nye proposed (1959, p. 287) for a direct measure of ʽeffective litter decay. It should be noted, however, that the term F_E in their paper refers to the steadily rising curve in Fig. 2b (including a *fraction* of the current year's litter, and some older material), not strictly material which had been subject to one or more years of decay (*cf.* Jenny et al. 1949).

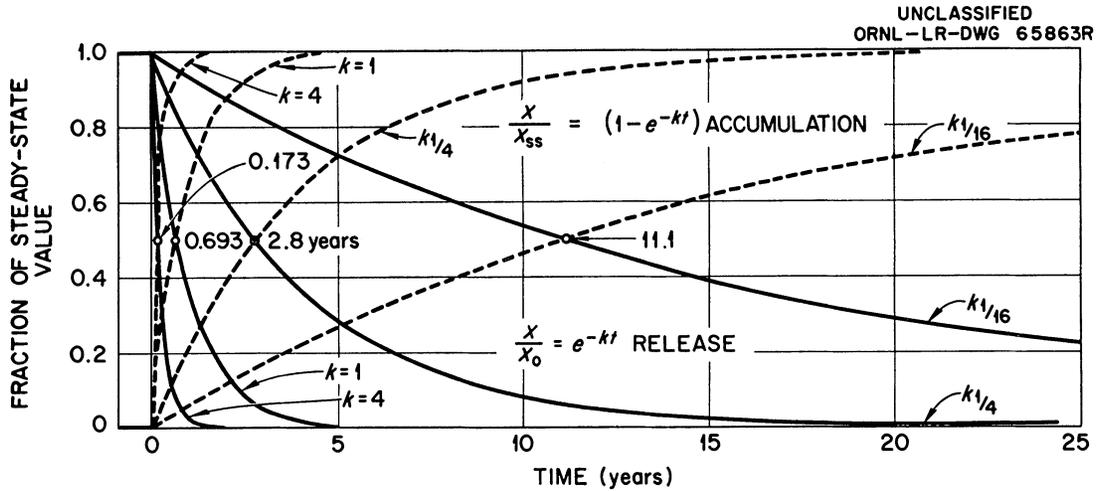For both deciduous and coniferous forests, of

FIG. 3. Exponential equations for carbon or energy stored in dead organic matter in a model ecosystem, for four values of $k = 4$, 1, 1/4, and 1/16 for very high, high, medium, and low decay rates, respectively. Solid lines for decrease from steady state, assuming production drops from L units per year to 0 at time $t = 0$. Dashed lines for accumulation toward steady state, where production is continuous at L units per year after $t = 0$.

course, litter fall is actually spread over a period of time. Both the peaks and valleys of the stair-step curve should be rounded off to something like the form shown by the short dotted lines of Fig. 4. Periodic litter inputs that are not discrete are suggested elsewhere as a better approximation compromising between two extremes of case 1 and case 2 (Neel and Olson 1962), but the extreme cases suffice for discussion of the illustrative data in the present paper. Other important limitations on the assumption of year-to-year uniformity of L and k are acknowledged as noted below, and can be overcome by elaboration of the mathematics or by the aid of computer techniques (Neel and Olson 1962, Olson 1963). However, these objections do not invalidate the basic ideas of the models or the kinds of conclusions drawn by Jenny et al. (1949) and by Greenland and Nye (1959).

RESULTS ON ESTIMATING DECOMPOSITION PARAMETERS

The estimates of k (from equation (4)) range from high values near $k = 4$ for the African forests, down to about 1 for two forests from Columbia. Pine forests of southeastern United States have values scattering around the line for $k = 0.25$ (1/4), while Minnesota pine forests range down toward the line for $k = 0.0625$ (1/16). Jenny et al. (1949) emphasized the high accumulation of litter in the California profiles and very slow decay parameters, down to 0.009 for lodgepole pine at 3,000 m altitude. Because such a small fraction of any one year's production is spent in decomposition during early stages of forest floor accumulation, storage of organic matter and of energy must continue until the total becomes so large that the product kX gradually approaches the income L and approximates the balance in equation (3). The time required for such an adjustment is considered next.

DURATIONS AND LEVELS OF ACCUMULATION

A convenient virtue of the simple exponential model is that the time required to reach halfway to the asymptotic level is the same time as that required for decomposition of half of the accumulated organic matter (Fig. 3). For either equation (9), (14), (15), or (16), this time is given by the solution of $0.5 = e^{-kt}$ for t, which is $-\ln(0.5)/k = 0.693/k$. We have an analogy with radioactive half-life, or half-time for accumu-
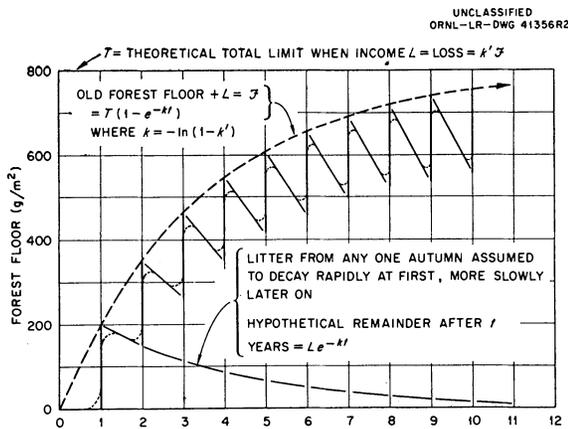
FIG. 4. Exponential decay and accumulation curves for idealized deciduous forest, with sudden annual litterfall of $L = 200$ g/m², and annual decomposition $k' = 1 - e^{-k} = 0.25$ of total present at any one time, so $k = 0.288$.

lation of radioactive materials. Another analogy is with "biological half-time" for either the elimination or the accumulation of materials in organisms or organs. The parameter $0.693/k = T_{0.5}$ may be viewed as a "half-time" for environmental accumulation or decay. Such half-times may be useful descriptive parameters, even in cases where an exponential model is not strictly applicable.

If an exponential model is valid, the time period $3/k$ should be that required for attaining 95% of the final level, while $5/k$ should approximate time needed to reach 99% of the final level. The reciprocal $1/k$ is the time required for decomposition to the fraction $1/e = 0.368$ of the initial level, or accumulation to $1 - 1/e = 0.632$ of the final level (see Fig. 3). This reciprocal can be viewed as the "time constant" for the component of an ecosystem circuit, analogous with that for discharging or charging of a condenser in a simple electrical circuit or in the integrator of an analog computer.

Such numbers are readily obtainable from tables of exponentials or logarithms, and a few have been selected in Tables I and II to represent the range

TABLE I. Parameters for exponential accumulation of organic matter or energy in ecosystems with steady litterfall rate (L)

Decay Parameters		"Half-time"	95% time	Steady-state Level for Production of L Units Per Year L/K			
$k = \frac{L}{X_{ss}}$	$\frac{1}{k} = \frac{X_{ss}}{L}$	$\frac{0.6931}{k}$	$\frac{3}{k}$	$L=50$	$L=100$	$L=200$	$L=400$
4	0.25	0.173	0.75	12.5	25	50	100
2	0.5	0.346	1.50	25	50	100	200
1	1.0	0.693	3.0	50	100	200	400
0.693	1.442	1.000	4.33	72	144	289	577
0.5	2	1.386	6	100	200	400	800
0.25	4	2.772	12	200	400	800	1,600
0.125	8	5.544	24	400	800	1,600	3,200
0.0625	16	11.09	48	800	1,600	3,200	6,400
0.0312	32	22.21	96	1,600	3,200	6,400	12,800
0.0156	64	44.42	192	3,200	6,400	12,800	25,600
0.01	100	69.31	300	5,000	10,000	20,000	40,000
0.003	333	232.3	1,000	15,000	30,000	60,000	120,000
0.001	1,000	693.1	3,000	50,000	100,000	200,000	400,000

of values particularly important for organic matter decay for cases 1 and 2 discussed above.

Figs. 5-7 provide illustrations of the great differences in the levels of accumulation and the promptness of equilibration to be expected for various combinations of productivity and decay parameters. Values of k plotted here are for the idealized maximum accumulation immediately following litter fall in a deciduous forest case from Table II. Comparison with Table I suggests that numerically the differences between deciduous and evergreen forests would not be great, especially for values of k or k' below about 0.06 or 0.016 which are shown in Figs. 6 and 7. For values

TABLE II. Parameters for seasonal accumulation and decay of organic litter, with sudden litterfall of L units, once each year (idealized deciduous forest)

Decay Parameters			Time Parameters		Seasonal Maxima and Seasonal Minima			
k	$k' = \frac{1}{1-e^{-k}}$	$\frac{1}{k} = \frac{L+F_{ss}}{L}$	$\frac{0.6931}{k}$	$\frac{3}{k}$	For $L=200$		For $L=400$	
					F_{ss}	F_{ss}	F_{ss}	F_{ss}
4	0.9717	1.010	0.173	0.75	204	4	407	7
2	0.865	1.156	0.346	1.50	231	31	462	62
1	0.632	1.582	0.693	3.00	316	116	632	232
0.693	0.50	2	1.00	4.33	400	200	800	400
0.288	0.25	4	2.41	10.4	800	600	1,600	1,200
0.136	0.125	8	5.19	22.5	1,600	1,400	3,200	2,800
0.0645	0.0625	16	10.7	46.5	3,200	3,000	6,400	6,000
0.0317	0.0312	32	21.8	94.5	6,400	6,200	12,800	12,800
0.0157	0.0156	64	44.0	190.5	12,800	12,600	25,600	25,200
0.0100	0.0100	100	69.3	300	20,000	19,800	40,000	39,600

higher than 0.1, numerical differences between k and k' become greater. The sawtooth character of the accumulation curve whose peak values are shown in Fig. 5 ($k' = 0.25$, $k = 0.288$) were already brought out on a larger scale, in Fig. 4.

DISCUSSION

The rate parameter k in part measures the effectiveness of decomposer organisms like fungi, bacteria, and certain animals in breaking down organic materials. Some of this breakdown of litter, accumulated on top of mineral soil, involves leaching and physical transport of materials into the mineral soil, providing income of carbon and energy for soil organic matter. But a large fraction presumably represents losses of energy from the ecosystem due to respiration of the decomposing organisms. These must be considered in the energy budget of the ecosystem as a whole.

At the 1959 Symposium on "Energy Flow in Ecosystems" at Pennsylvania State University, where this paper was presented, differences between aquatic and terrestrial systems and between the approaches of the workers investigating them were emphasized by several papers. The first two papers by Beyers (1962) and by Wilson illustrated progress and difficulties in the use of several methods aiming at direct measurement of rates of oxygen and CO_2 exchange and C^{14} uptake from which limnologists and oceanographers infer rates of energy flow. In planktonic microcosms decomposition rates and energy turnover are presumably high. But there is nevertheless deposition and accumulation of resistant organic materials in bottom sediments in many environments. This results in a "litter decay" situation and storage of sedimentary carbon somewhat analogous with that considered here for terrestrial systems.

The third paper (see Ovington 1957, 1961, Ovington and Heitkamp 1960) illustrated the
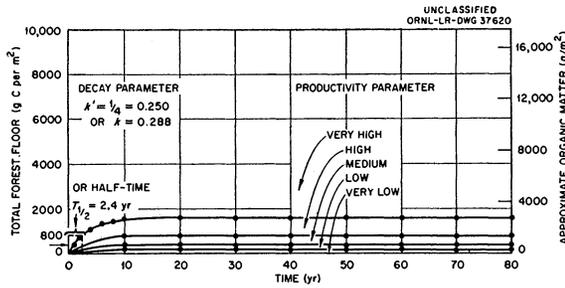
FIG. 5. Increase in annual "autumn maximum" of dead organic matter on top of mineral soil for several levels of litter productivity parameter L, for idealized deciduous forest. Medium decay rates, k and k'.
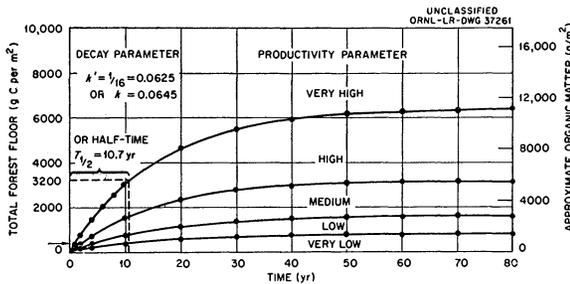

FIG. 6. Increase in anual "autumn maximum" of dead organic matter on top of mineral soil for several levels of litter productivity parameter L, for idealized deciduous forest. Low decay rates.
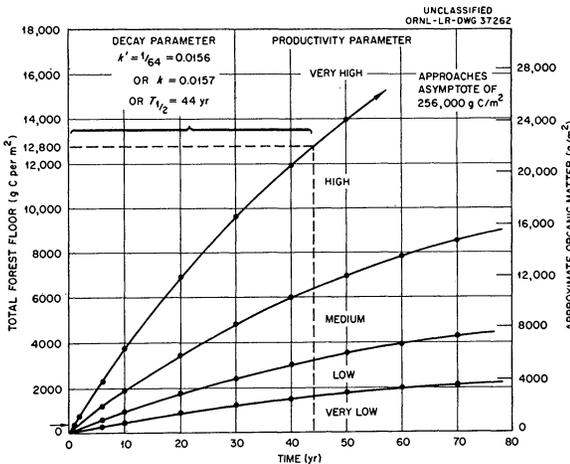

FIG. 7. Increase in annual "autumn maximum" of dead organic matter on top of mineral soil for several levels of litter productivity parameter L, for idealized deciduous forest. Very low decay rates. Note great differences in both the asymptotic accumulation level and the promptness of attaining this level; also the similarity of k and k' in Figs. 6 and 7.

contrasting approach of terrestrial harvest studies, typically measuring the accumulated net production and calculating average rates of energy flow over increments of time. Ovington estimated that over half of the net production during the development of a 55-year-old pine forest had been re-

leased by decomposition. The relative importance of the decomposer pathways of energy flow was even greater in younger forests and herbaceous ecosystems.

Implications for net production and succession

Present illustrations show the wide variation in the period during which the ecosystem as a whole may show a positive net storage (production minus loss) of energy in the form of dead organic matter, unincorporated in mineral soil. Thick humus layers in many northern regions require many decades to develop. Even longer durations will normally be required for equilibration of production and loss of organic matter or humus within the mineral soil. For example, rates of accumulation of soil nitrogen and humus in sand dune soils of approximately known ages indicated values of k near 0.003, so that $3/k$ or about 1,000 years would be needed to attain 95% of the steady-state level (Olson 1958). Depending on what assumptions are made about contributions of organic matter to the mineral soil from the forest floor and roots (cf. Jenny 1950, vs. Greenland and Nye 1959), decomposition rates for soil organic matter in many other soils may show similar lags in accumulation. Even maximum estimates involve only a few per cent decay per year, so $3/k$ is of the order of centuries.

Considering the total development of an ecosystem, a "climax" condition in the sense of a steady state, or zero net community storage of matter or energy, may not be attained until long after composition and average biomass of many living species has become nearly constant, or begun to oscillate around some average value.

One aspect of natural community development involves the readjustment of all components of an ecosystem toward an asymptotic condition. The condition approached is influenced by a given set of values for the productivity and decay parameters. Some biological developments may be specifically delayed until litter and soil humus have approached near their steady-state values.

A second aspect of developmental succession involves gradual or sudden changes in levels of production or rates of decay, controlled by the presence of new species of plants or animals, and new physical and chemical characteristics of the materials they produce. A typical succession may thus involve alternating episodes of adjustment toward specific levels and fairly sudden shifts when the parameters governing these levels change, as illustrated by E. P. Odum (1960). Slow and sudden changes in soil, which are regulated by parameters for losses of materials from the soil,

may both contribute to long-term trends in succession.

As noted earlier (Olson 1958), quantitative models for changes in community succession and soil development can thereby impart a mathematical significance to Cowles's classic statement (1899) : that succession represents a "variable approaching a variable, rather than a constant." The first variable consists of the vector sum of properties describing the state of the ecosystem. The second variable includes the asymptotic condition which is being approached during a given phase of development, and the parameters like L and k which govern the level of this condition. While the first variable may change rapidly at first, then slowly for a while as it approaches a steady state (or oscillates around it), a change in the second variable and the parameters which govern it will bring the whole system into a new period of readjustment.

Modifications of models

The assumptions of constant production and constant decomposition parameters will accordingly have to be modified to treat many special cases. One change is the allowance for low production during early stages of population development and succession, and a positive feedback to favor higher productivity as growth and development proceed. The result is a sigmoid curve pattern for accumulation of living organic matter, litter, and incorporated humus like the analog computer graphs of Neel and Olson (1962). H. T. Odum's paper (1960) on electrical network analogs did not account for any condition other than the steady state. It could be extended to the accumulations through time by the addition of capacitors into his circuit.[3]

Some aquatic systems and bogs (Lindeman 1942) have prolonged accumulation of peat or other biogenic sediments, where decomposition may be even slower than in any of the terrestrial systems. Some important ecosystems may share characteristics of terrestrial and aquatic communities and are modified by import and export of energy and materials by means of water currents, as noted in the papers on salt marshes by Smalley (1960) and Kuenzler (1961) (see also Odum and Smalley 1959). Their data on invertebrate herbivores and Golley's (1960) on vertebrates also show that a measurable but fairly small fraction of energy flow passes through consumers as com-

[3] This modification which I suggested to Odum in March 1959 has been made in his later electrical analog network. It introduces a positive feedback by manually charging the production parameter.

pared with that through decomposers, except in systems that are heavily grazed.

Decomposition may be so slow as to require a modification in the model for aquatic systems because of the possible failure to level off at any constant asymptote. If organic matter is essentially removed from access to decomposers during burial in bottom sediments, a given vertical column through the ecosystem extending down through these sediments may show the continued storage of energy in the forms which ultimately contribute to our fossil fuels of peat, coal, petroleum, or oil shale.

A particularly interesting case of the changing parameters mentioned earlier involves the increase in decomposition rate after early stages in community development or succession have passed. This often results in the breakdown of thick forest floor accumulations which commonly occur in first-generation conifer forests in many ecological successions. While lower storage of energy and mineral nutrients may be found in later successional stages (often deciduous or mixed forests), the faster turnover of the nutrient elements may permit the primary productivity of the system to be higher than before. On the other hand, there may be developments of succession which actually represent a degeneration, if the losses of important nutrients or of the favorable physical characteristics of organic humus proceed so rapidly that they cannot be balanced by production.

The equations outlined above are given in terms of deterministic models and are analogous with the differential equations and solutions in physics. Even for physical models (as in radioactive decay, for example) there are chance fluctuations which make these equations only approximations to what happens in reality. We could similarly visualize many complicating chance variables which could make the actual state of any given ecosystem fluctuate around the hypothetical conditions which are here projected on the basis of a simple model. In addition to chance fluctuations, there are important oscillations (besides the abrupt seasonal stops indicated in Fig. 2) which might be superimposed on the simple trends given here, and some of these are covered elsewhere (Neel and Olson 1962).

These further developments can be handled by direct extension of the simple differential equations and exponential equations used here. They are facilitated by the use of analog computers which perform the integrations electrically or electronically (Olson 1963). Furthermore, the use of computer components aids the connection of many components into a whole electrical or electronic

circuit to simulate the trophic structure of the ecosystem. The physical operations simulating integration sidestep many of the complications in the analytical representation of integrals arising when the outputs of some components of the system serve as inputs to the next components (Neel and Olson 1962, Appendix). While the individual components might follow a simple exponential development controlled by income and loss, as in Figs. 2-7 if their inputs were constant, the various lags in the build-up of inputs to different parts of the system can be allowed for in the behavior of the analog model.

SUMMARY

While some fraction of the solar energy fixed by producing plants is released by respiration of these plants and of animals, much of it is stored in dead organic matter until released by decomposing organisms, at rates which vary greatly from place to place. The general differential equation for the rate of change in energy storage is illustrated by models for build-up and decomposition of organic matter, particularly for litter in deciduous or evergreen forests. Equations of Jenny et al. (1949) and Greenland and Nye (1959) each have a useful place in estimating decay parameters. For the case of steady production and decay, the ratio of annual litter production, L, to the amount accumulated on top of mineral soil in a steady state, X_{ss}, provides estimates of the decomposition parameter k. Estimates range from over 4 in certain tropical forests to less than 0.01 in subalpine forests. Decomposition rates for organic matter within mineral soils may range from near 0.01 to 0.001.

Since it takes a period of about $3/k$ years before storage has attained 95% of its steady-state level, many ecosystems continue to show a positive net community production for centuries—perhaps long after changes in numbers and biomass of some species are reduced to minor fluctuations around a "climax" composition. On the other hand, the slow change in soil conditions may in some cases facilitate the introduction of new species after some delay during succession. The change in productivity or decomposition parameters controlled by these species may lead in turn to a series of later readjustments in energy storage and release, which modify litter and soil conditions. Modified microenvironments in turn may further alter the succession and "climax."

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ECOLOGY OF WATER-LEVEL MANIPULATIONS ON A NORTHERN MARSH[1]

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INTRODUCTION

In recent years the deliberate drawdown technique has become widely used for managing waterfowl and muskrat marshes (Addy and MacNamara 1948, Uhler 1956). The Agassiz National Refuge in northwestern Minnesota has been the scene of an extensive program of this type. Here, following the original flooding in 1939 and 1940, large areas of open water had been created by the gradual disappearance of emergent vegetation, although some beds of hard-stem bulrush and reed persisted in the middle of two pools where mineral soil was present. The destruction of these emergent marshes reduced nesting habitat for diving ducks; waterfowl brood and moulting cover; favorable muskrat habitat; and had exposed the dikes to greater erosion by wave action.

A program of water-level manipulations to establish emergent vegetation was conducted in this area between 1949 and 1957. This planned program of drawdowns, with the revegetation of open-water areas as the primary objective, resulted from observations of the invasion by emergents and annual weeds of mud flats formed in 1949 and 1951 when two pools were drained to allow dike repairs.

During the growing seasons of 1953 and 1954, the senior author made an intensive study of the ecological changes associated with these drawdowns (Harris 1957). Refuge personnel cooperated in extending the work through the 1955, 1956, and 1957 seasons. Throughout this report the term "drawdown" applies to the reduction of water levels for 1 or more years, and the restoration of levels is termed "reflooding."

A survey of the literature shows that various authors have mentioned the detrimental effects that prolonged stabilized water levels have on most species of emergent aquatics (Uhler 1944, Penfound and Schneidau 1945, Sharp 1951, Martin 1953, McDonald 1955). Other workers have pointed out that drawdown operations are useful in the production and utilization of crops of annual food plants such as millets and smartweeds (Bellrose 1941, Pirnie 1941, Griffith 1948, Schmidt 1951, Crail 1951). Stearns, MacCreany, and Daigh (1940) and Cottam and Bourn (1952) have discussed plant succession on drained lakes. Lynch, O'Niel, and Lay (1947), McLeod (1949), Baldwin (1950), and Martin (1953) all have mentioned that many emergent aquatics require bare mud flats for successful germination and seedling establishment. The use of the drawdown technique in a planned program of perennial emergent management has been discussed by Errington (1948), Schmidt (1953), Nelson (1954, 1955), and Uhler (1956). Recently Kadlec (1962) has reported in detail on a drawdown carried out in 1958 by the Michigan Department of Conservation.

THE STUDY AREA

The Agassiz National Wildlife Refuge lies in the ecotone between the grassland and coniferous forest in northwestern Minnesota. The more than 60,000 acres of the refuge vary only about 20 feet in elevation. The mineral soil, a slightly alkaline clay-sand, is overlain in many places with considerable peat. Much original peat was removed by fire when the entire region was drained and farmed between 1911 and 1937 (Hunt and Mangus 1954). In some parts of the refuge, the bare mineral soil is now exposed; in other parts the