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ECOLOGICAL SCIENCES DIVISION

ANNUAL PROGRESS REPORT

Period Ending September 30, 1971

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ECOLOGICAL SCIENCES DIVISION
ANNUAL PROGRESS REPORT
For Period ending September 30, 1971

S. I. Auerbach, Director
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OAK RIDGE NATIONAL LABORATORY
Oak Ridge, Tennessee 37830
operated by
UNION CARBIDE CORPORATION
for the
U.S. ATOMIC ENERGY COMMISSION

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Summary

Several sections of the Annual Report are abbreviated because of the preparation of environmental impact statements. The project areas represented by complete reports are summarized below.

1. RADIONUCLIDE CYCLING IN TERRESTRIAL ENVIRONMENTS

Terrestrial environments may receive radioactivity from various sources of nuclear technology, that is, weapons testing, nuclear excavation, natural resource stimulation, waste processing, reactor power plants, and conceivably from transportation accidents. A major mission of the Ecological Sciences Division has been to study the fate of fission products and other radionuclides in different ecosystems. Research is designed to determine the mobility of radionuclides in major segments of the terrestrial environments. Reciprocal transfers of environmental radioactivity is investigated for three major components — soil, plant, and animal — of forested and grassland ecosystems. Pathways and rates of radionuclide transfer first are elucidated with manipulated microcosms, and then results are validated in large-scale field-plot and ecosystems experiments. Investigation of radionuclide behavior at the atmosphere-plant and soil-plant interfaces help to explain how hazardous materials enter food-chain pathways of movement. A vast array of animal life then interacts with plants and soil to cause food-chain movement of radioactivity, thereby causing either a concentration or dilution of materials through trophic exchanges. With the aid of integrative systems ecology techniques, data on radionuclide transport between soil-plant and animal components are modeled to illustrate the flux of radionuclides in ecosystems.

Research results on retention and weathering of fallout-simulant particles by grass indicated an initial rapid loss rate ($T_{1/2} = 4$ to 5 days). Redistributed particles eventually became trapped in the litter mat of the turf grass vegetation, and over half the particles remained in contact with biotic components for 50 days. A simulation based on data from several experi-

ments on grass contamination with a fallout simulant illustrated that the radiocesium content of living foliage diminished rapidly, dead vegetation remained contaminated for the longest time interval, plant uptake from soil was several orders of magnitude greater than direct foliar contamination, and soil served as a sink for radiocesium. Other studies of radionuclide cycling include direct plant-to-plant transfer of radiocesium, where results on rainout transfer of radiocesium from tree to ground cover indicated that foliar absorption can be a major pathway for movement of some radionuclides between the canopy and understory vegetation. Other tracer experiments with tritium have further characterized the water cycle in the forest ecosystem, and accurate information on the dynamics of this cycle will further aid other evaluations of radionuclide mobility on the landscape.

Research on soil chemistry and reciprocal root-soil transfers continue to provide information on long-term availability of radionuclides to ecological and human food chains. From an initial pulse input of radiocesium to the rooting zone of a forest soil, the nuclide has gradually become uniformly distributed throughout several soil horizons over a seven-year period. Chemical exchanges, leaching, and mixing by soil animals were the processes responsible for redistribution. Ultracentrifugation techniques, which were developed in studies of radioisotope distribution on clay minerals, will be applied to new research on questions of soil chemistry and transport of plutonium in humic soils.

Research on food-chain transport of radionuclides by arthropods has revealed that many transfers result in discrimination rather than concentration of radioactivity. While concentration of radionuclides may be negligible in arthropod food chains, high feeding, elimination, and population turnover rates can significantly enhance the cycling of radioactivity in terrestrial environments. In other food-chain studies tracers have been employed to determine food preferences and feeding rates of the shrew and white-footed mouse in their native habitats. Such experimental data on radionuclide behavior in ecosystems is invaluable for predict-

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ing the fate of radioactive waste in complex ecological systems.

2. WALKER BRANCH WATERSHED: A STUDY OF TERRESTRIAL AND AQUATIC SYSTEM INTERACTION

Objectives of the Walker Branch watershed project are: (1) to quantify the relationships between terrestrial and aquatic productivity, mineral balance, and water quality in a natural forested ecosystem and (2) to quantitatively assess the impact of a relatively new silvicultural technique, forest fertilization, on these relationships. These objectives are consistent with those of the International Biological Program (IBP). Therefore, studies on Walker Branch watershed provide input to IBP research in the areas of primary production, mineral cycling, and land-water interaction.

Characterization of the drainage basin is addressed in two studies. The first, a geology survey, resulted in a detailed surficial geology map of the watershed. The other study reconstructed the past history of the watershed, including land management practices on the watershed prior to acquisition by AEC. Both studies provide information necessary for interpretation of terrestrial research projects and analyses of hydrologic data.

Remeasurement of the 298 permanent growth plots on the watershed revealed that of the four forest types basal area increases were greatest for chestnut oak stands, followed by those of oak-hickory and mesophytic hardwoods, while pine stands decreased in basal area. Preliminary summaries for biomass production and mortality are also presented. Seasonal patterns of nitrogen, phosphorus, potassium, and calcium concentrations in foliage of ten tree species are shown together with quantities of these nutrients returned to the forest floor in litterfall. Preliminary estimates of litter biomass are presented for the O₁ and O₂ soil horizons.

A brief description of a soil moisture and evapotranspiration simulation model is introduced in this report.

The model operates in response to meteorological inputs and will be used to correlate hydrologic response with forest growth and nutrient movement patterns on Walker Branch watershed.

4. INTERNATIONAL BIOLOGICAL PROGRAM: OAK RIDGE RESEARCH SITE

Ecosystem dynamics, land-water interactions, and the governing internal mechanisms are the delicately balanced processes which we strive to understand as man continues to manipulate his environment. The Oak Ridge Site of the U.S. IBP Eastern Deciduous Forest Biome proposes as its unique contribution the analysis of landscape interactions based on research and modeling implemented at hierarchical levels of resolution. Simultaneous development of the level of processes and components of specific ecosystems permits evaluation of the significances of these processes and consequences of their modification and alteration to total system behavior. Information on the basic production processes which regulate forest ecosystems is being obtained to provide comparative data on the efficiencies of alternative choices of land use in terms of solar energy conversion, biomass production, and mineral utilization. Rates of transfer of energy and materials among the components of these systems are being identified and quantified. Emphasis is being placed on the concomitant development of (1) mechanistic process models (e.g., photosynthesis, nitrogen mineralization, insect consumption), (2) the coupling of process models leading to construction of dynamic stand models (ecosystem models of carbon, nutrient elements, and water), and (3) the integration of stand models for the development of predictive models of watersheds. Significant scientific contributions in basic research and systems modeling are being made at each level of resolution, and the integrated research program is designed to ensure the maximum degree of synthesis.

1. Radionuclide Cycling in Terrestrial Ecosystems

R. C. Dahlman³

T. Cox ¹	R. E. Gaskins ⁷	J. S. Olson ³	J. D. Story ³
S. L. Deal ²	W. F. Harris ³	R. V. O'Neill ³	F. G. Taylor ³
B. E. Dinger ³	G. S. Henderson ³	M. G. Nielsen ⁶	R. I. Van Hook ³
G. J. Dodson ³	M. Hogland ⁴	L. N. Peters ³	J. P. Witherspoon ¹
P. B. Dunaway ³	L. K. Mann ³	D. E. Reichle ³	M. Wittkamp
C. W. Francis ³	J. B. Mathies ⁵	M. H. Shanks ³	
M. L. Frank	J. F. McBrayer ¹	P. Sollins ¹	

SCOPE

The terrestrial environment may potentially receive radioactivity from different nuclear technologies such as weapons testing, nuclear excavation or stimulation, waste processing, and conceivably transportation accidents. Historically, the mission of the Ecological Sciences Division has been to study the fate of fission products in different environmental systems. Radionuclide cycling investigations have focused on total ecosystems where prior field and laboratory research efforts have identified clues to the behavior of fission products such as ⁹⁰Sr and ¹³⁷Cs in terrestrial ecosystems. Information gained from these investigations has fostered enhanced understanding of ecosystem function and has led to an improved ability to predict the fate of radioactivity in both forest and grassland ecosystems. As these investigations have refined the data base on the dynamics of radionuclides in ecosystems, the capability for predicting the fate of contaminants in the environment has improved correspondingly.

Successful determination of the fate of radioactivity in the landscape requires an understanding of the

pathways through which fluxes of contaminants may move. By coupling process mechanisms and flux kinetics with environmental pathways, our objective is to predict rates of radionuclide movement and resultant hazards to endemic organisms, including man, for important segments of our environment. Research activities, which provide the data base for predicting radionuclide dynamics, are organized around principal components of the ecosystem. We address research questions to the reciprocal interactions of these components and the interfacing of major environmental sectors. Atmosphere-plant and soil-plant interfaces play a major role in determining nuclide behavior in landscapes, and a vast array of animal life interacts with plants and soil to cause food-chain movement of radioactivity. Research on mechanisms of transport at points where plants interface with either atmosphere or soil sources of contamination provide estimates of input terms for evaluating radionuclide movement through food chains. By coupling this information with integrative systems ecology techniques, the flux of radionuclides can be traced through environmental systems. This phase of our research requires a strong interaction between research efforts in radionuclide cycling and modeling in systems ecology.

The ability to predict the flow of radionuclides through ecosystems also is aided by concurrent work on basic ecological processes in other programs in the Ecological Sciences Division. These are field and laboratory studies on watershed-aquatic interactions and ecosystem studies of the International Biological Program. Such programs provide data on biological pro-

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activity, mineral, and hydrologic cycles in ecosystems, which are the basic mechanisms by which contaminants move in the environment. The supporting information on mineral element dynamics strengthens our ability to assess impacts on sensitive organisms and dose commitment to man from radionuclide releases to the environment. Specific research results on radionuclide cycling are organized around situations of plant interfaces with the atmosphere and soil and around dynamics of radionuclides in food chains.

Microcosm research is a unique experimental tool for gaining insight into fluxes of hazardous nuclides and nutrient elements in ecological systems. Physically the microcosms consist of manageable systems which contain measured amounts of components and materials characteristic of the natural environment and in proportion to their field occurrence. The components may be nonbiological such as soil, sediments, water, and air, and biological such as monospecific or mixed natural populations of microbes, algae, plants, insects, etc. Behavioral characteristics of the systems are studied by manipulating complexity, that is, by adding or taking out one or more components and by modifying environmental conditions such as temperature, moisture, nutrient content, etc. The impact of components and environmental factor manipulation on pathways and fluxes of toxic materials and nutrients can be assessed in systems of varying complexity.

PLANT-ATMOSPHERE RELATIONS

R. C. Dahman

B. E. Dinger	L. N. Peters
W. F. Harris	P. Sollins
G. S. Henderson	F. G. Taylor
L. Mana	J. P. Witherspoon

Radioactivity releases to the atmosphere usually impinge on the vegetative component of ecosystems. Plant interception of either particulate or gaseous contaminants constitutes one source of entry of hazardous materials into food chains which ultimately can lead to man. Alternatively, through the canopy-transpiration process, plants can redistribute a radionuclide such as tritium to the atmosphere as water vapor. Consequently, vegetation may function as an interceptor or recirculator of radioactivity in the environment. It is important, then, to know magnitudes of nuclide movement across plant atmosphere interfaces in the examination of environmental and radiological hazards. Research results are presented for particle retention by vegetation and for subsequent weathering

of the particles following initial deposition. Transport and dissipation of an acute dose of tritium in deciduous trees provide another example of radionuclide movement at the vegetation atmosphere interface. Direct transfer of radiocesium from the overstory canopy to understory vegetation via rainfall is another example of a highly mobile cycling process.

Retention of Simulated Fallout Particles by Plants

Early retention and weathering rates of fallout particles in pasture, forage, and turf grasses characterize initial cycling processes in a contamination event. Initial retention values and early weathering losses are also very important in beta radiation dose estimation, since the major portion of the total dose is delivered during a short interval of time following fallout deposition. Long-term retention influences the magnitude of radionuclide transfer through food chains. This is particularly true for grass species which are consumed by grazing livestock. Kentucky-31 fescue (*Festuca arundinacea* Shreb.), common Kentucky bluegrass (*Poa pratensis*), Bermuda grass (*Cynodon dactylon*) and zoysia (*Zoysia japonica*) were selected for experiments on retention and weathering because these grasses have a wide geographic distribution and economic importance, and they possess varied foliage morphologies and exhibit different foliage densities. These grasses are commonly used both as pasture and turf, except zoysia which is used only for turf.

Replicated areas of each grass were established in field plots and maintained at heights and densities which are typical for each species. Quartz fallout simulant particles (44 to 88 μ diam) tagged with 0.56 μ Ci of $^{134}\text{Cs}/2$ were applied to each plot at a mass loading of 1.85 g/ft². The particles were applied with an elevated spreader apparatus which had been developed at ORNL for fallout studies in a grassland.⁸ Initial retention and weathering losses were determined from radioassay of foliage samples over the 0.5- to 48-day postcontaminant period.

Initial retention values for the four species were not significantly different from each other (Table 1.1). Average initial retention (F) for all grasses was 77% of the amount applied to the ground surface. Morphological differences between these four grasses caused no large variation in initial particle retention. Differences between particle retention values for grasses at subsequent sampling periods were nominal, and a single curve

8. R. C. Dahman et al., pp. 153-65 in *Environmental Contamination by Radioactive Materials*, IAEA, STI/PUB/226.

Table 1.1. Initial interception of 44- to 88- μ fallout particles by grass foliage

Grass	Initial retention (C_p) ($\mu\text{Ci/g}$)	Initial deposition (m_p) ($\mu\text{Ci/ft}^2$)	Contamination factor (a_p) (C_p/m_p)	Plant density (W_L) (g/ft^2)	Fraction intercepted (F) (a_p/W_L)
Fescue	0.032	1.926	0.017	40.43	0.687
Bluegrass	0.028	1.882	0.015	52.87	0.793
Bermuda	0.029	1.730	0.017	48.23	0.820
Zoysia	0.021	1.837	0.011	69.59	0.765

(Fig. 1.1) adequately described particle retention as a function of time. Retention decreased from 77 to 14% in 14 days. The initial decrease to 46% (t_2 , Fig. 1.1) was attributed to redistribution by wind action because the field plots received no precipitation during this period. Ten rain periods were recorded and total rainfall was 6.76 in., but rainfall had a negligible effect on particle weathering.

A decrease in retention of particles by foliage resulted in particle accumulation in the grass mat as shown in Fig. 1.1. At the $t_{0.5}$ measurement, approximately 19% of the applied particles were retained in the mat, and after 14 days the mat contained 55% of the initial fallout simulant. The mat content remained at this level for the remainder of the experiment. Including both the grass foliage and mat particle retention, there was an average initial retention of 96%, and this amount decreased to 69% after 48 days. These results indicated that turf grass foliage and littermat can retain particle fallout very effectively for substantial periods after a simulated contamination event. Over half the particles remained in contact with biotic components for 50 days, and this quantity would be readily available for entry to food chains, thereby increasing hazards to endemic organisms and man from radiation exposure. Extended retention of high specific activity particles also could manifest increased beta radiation dose to sensitive plant parts.

Retention of Simulated Fallout by Agricultural Plants

Initial retention and weathering loss of dry fallout particles (1 to 44 μ diam) by plants may be influenced by conspicuous differences in growth habit and foliage morphology. Retention and weathering processes were quantified for fallout simulant applications to soybean (*Glycine max* variety Lee) and grain sorghum (*Sorghum vulgare*). Six-week-old plants with heights ranging from 0.5 (soybeans) to 1 m (sorghum) were contaminated with a fallout simulant which consisted of siliceous flyash tagged with Cs . The nuclide was fixed on

Fig. 1.1 Average retention of 44- to 88- μ particles by grass foliage and mats and the amount of retained up to 48 days following deposition. Note that the mat retains most of the particles lost from foliage.

flyash with high-temperature treatment. Dry fallout simulant was applied to 25 plants of each species inside a plastic cylinder, a containment design which minimized wind dispersion during application. Mass loading was 1.96 g particles per square foot of soil surface area, and the activity was 13.65 $\mu\text{Ci/ft}^2$.

Foliage area and biomass relative to soil surface area were determined before simulant application. Immediately following contamination and at one-week intervals for 34 days, three plants of each species were randomly collected and analyzed radiometrically according to procedures reported elsewhere.⁹ Soybean plants inter-

9. J. P. Witherspoon, *Proceedings of Symposium for Survival of Food Crops and Livestock in the Event of Nuclear War*, AEC-CONF (in press).

Table 1.2. Initial retention of fallout particles by plant parts
Data are summarized according to Miller's contamination factor convention^a

	Initial deposition (m_p) ($\mu\text{Ci}/\text{ft}^2$)	Initial retention (C_p) ($\mu\text{Ci}/\text{g}$)	Contamination factor (a_p) (C_p/m_p)	Plant density (W_L) (g/ft^2)	Fraction intercepted (F) ($W_L a_p$)	Fraction of total initial retention (%)
Soybean	13.65					
Leaves		0.343	0.025	12.80	0.321	81.2
Stem		0.110	0.008	9.28	0.074	18.8
Total	13.65			22.08	0.395	
Sorghum	13.65					
Leaves		0.229	0.017	5.44	0.091	23.7
Stem		0.008	0.001	6.34	0.004	1.0
Axil		10.355	0.758	0.38	0.288	75.3
Total	13.65			12.16	0.383	

^aC. F. Miller, pp. 501-26 in *Radioecological Concentration Processes*, B. Abegg and F. P. Hungate (eds.), 1967.

cepted 39.5% of the initial deposition, and sorghum intercepted 38.3% (Table 1.2). Sites of interception varied considerably for the different plants. For soybeans 81.2% of the fallout initially intercepted was located on the foliage, but the foliage of sorghum held only 23.7% of the total quantity intercepted. Soybean stems were more effective in intercepting the fallout particles than were sorghum stems. Vertical, single stems of sorghum contained only 1% of the particles intercepted by the whole plant, while soybean stems contained 18.8%. The major site of initial particle interception in sorghum was the axil, the angular region where the leaf joins the stalk and forms a sheath.

Two components of loss were evident from a graph of particle retention vs time. Weathering half-times for particles were estimated from linear regression analyses on the 0- to 7- and 7- to 34-day components. The T_w 's (Table 1.3) for particles during the 0- to 7-day time component were very similar for plant parts of both species (3.4 to 4.4 days). For the longer component larger differences in T_w 's occurred between species and plant parts. Values for soybean foliage and stem were 1.3 and 1.2 times greater, respectively, than for foliage and stem of sorghum. Particles in the axils of sorghum had T_w 's twice that of particles on sorghum foliage.

It appears that half-time values for foliage of many different kinds of vegetation and different particle sizes may be similar. Values from the present study, in which particle size averaged only 7.5 μ diam, and those from other studies¹⁰ do not differ by much more than a

Table 1.3. Weathering half-times (T_w , days)
for simulated fallout particles retained
on soybean and sorghum plants

Plant part	T_w time component	
	0 to 7 days	7 to 34 days
Soybean foliage	4.44	24.40
Soybean stem	4.13	21.77
Sorghum foliage	3.98	17.93
Sorghum stalk	4.03	17.50
Sorghum axils	3.47	35.42

factor of 2 for periods after the first week postdeposition. It may be practical, therefore, in assessing the biological hazard of fallout to assume a weathering half-life range of 15 to 30 days for particles on foliage of field and vegetable crops during this period. This could be used in estimates of minimum and maximum retention times of fallout which is available for entry to food chains.

Mosses and Lichens

The tussock growth habit of mosses and lichens may form a dense cover over the soil surface in moist environments, and retention and weathering characteristics of particles deposited on these plants were determined in this investigation. Tussocks of cryptogamic plants, lichen [*Cladonia subterminalis* (Abb.) Evans] and moss (*Dicranum scoparium* Hedw.), were placed in the field and contaminated with a ¹³⁴Cs-tagged fallout simulant (88- to 175- μ -diam particle). The tussocks were trimmed to form disks of uniform

10. J. P. Witherspoon, *Proceedings of Symposium for Survival of Food Crops and Livestock in the Event of Nuclear War*, ABC-CONF (in press).

Dimensions prior to contamination. Immediately after particle deposition and at successive one-week intervals samples were randomly collected for radiometric analysis.

The results of initial retention are given in Table 1.4, and data are summarized according to Miller's¹¹ contamination factor convention. The lichen retained fallout in much the same manner as lawn grasses.¹² For example, the fraction (*F*) initially retained by lichens was similar (69.8%) to that reported for grass species (68 to 79%). Mosses, however, intercepted a much greater fraction (100%) as indicated in Table 1.4. Particle retention of approximately 100% by moss tussocks probably was related to the large foliage area per unit of soil area because each tussock has many individual plants. Numerous small leaves also comprise effective trapping sites for particles. Individual rainfall events seemed to have little effect on weathering loss (Fig. 1.2).

Weathering half-times for particles on whole plants or plant parts are important in radiation dose estimates

and possible entry of fission products into food chains. Weathering half-time components in this study differed from previous investigations in terms of a short component (0 to 1 day) and a single long component (1 to 42 days). Linear regression analysis of the longer time component was used to estimate the weathering half-times, which were 48.6 and 49.4 days for lichen and mosses, respectively. Particle retention for steppe plants were within a factor of 2 of those reported for the higher plants.¹³ The longer half-times probably were caused by the lodging of particles in the lichen-soil interface and moss-litter zones, similar to the fall from grass foliage to mat.

11. C. F. Miller, pp. 501-26 in *Radiological Contamination: Problems*.
12. See "Acute and Chronic Radiation Contamination of Ground Vegetation," this report.
13. V. P. Wilhemsson, *Proceedings of Symposium on the Role of Food Crops and Livestock in the Event of Nuclear War*, AEC-CONF (in press).

Table 1.4. Initial retention of fallout particles by lichen and moss tussocks.
Moss load was 5.0 g/ft², and total activity applied to each tussock was 3.5 μCi/ft².

Plant	Initial deposition (<i>m_p</i>) (μCi/ft ²)	Initial retention (<i>C_p</i>) (μCi/g)	Contamination factor (<i>a_p</i>) (<i>C_p/m_p</i>)	Plant density (<i>D_p</i>) (g/ft ²)	Initial retention factor (<i>F_p</i>) (<i>C_p/m_p</i>)
Lichen	3.50	0.0209	0.0059	118.30	0.000175
Moss	3.50	0.0523	0.0149	77.50	0.000191

Fig. 1.2. Initial fallout interception and retention by lichen and moss tussocks and relative weathering to 45 days post-application.

Lichen and moss are generally radioresistant, such that radiation doses to contaminated tussocks would result in no detectable effects. However, both organisms exhibit a low profile growth habit and have effective trapping sites for particles in plant-substrate interfaces. Meteorological events, important to particle retention in previous studies (wind), would have little influence on the amount retained by lichens and mosses. Weathering half-times, however, are important from the standpoint of possible entry of fission products into food chains. Fallout studies with similar lichens (*Cladonia*) in the arctic have focused on radionuclide concentrations in food chains, and our results on long-term retention provide additional insight on reasons for higher radiocesium concentrations in the lichen-caribou-Eskimo food chain. Contaminants are effectively retained on the caribou forage (lichen). However, once particles become dislodged from the fruticose structures they are effectively contained at the soil-plant interface, and would only be subject to redistribution by surface water runoff.

Acute and Chronic Radiocesium Contamination of Grassland Vegetation

From numerous observations of foliar interception of fallout radioactivity, there are strong indications that this mode of contamination will result in higher concentrations in foliage and foodstuff compared with radionuclide uptake from soil.¹⁴⁻¹⁵ When fallout simulant particles were deposited directly on fescue (*Festuca arundinacea* Shreb.), the ¹³⁷Cs content of living vegetation was two orders of magnitude greater than when the radionuclide was assimilated from an equivalent soil pool. The initially high radionuclide concentrations of foliage, due to direct deposition, decreased exponentially as a function of time after the contamination event. Substantial radioactivity concentration in vegetation creates a relatively high hazard to other animals which may feed on the contaminated material during initial postcontamination periods. However, the high hazard potential is of relatively short duration, because weathering and growth processes decrease radionuclide concentrations to a level which is maintained by uptake from soil. Subsequently, a lower equilibrium between plants and soil becomes established, and chronic plant burdens are a function of routine plant nutrition processes and the quantity of radionuclide in the soil

pool. Concentrations maintained by this equilibrium are several orders of magnitude less than the initial concentration caused by direct deposition on foliage. The chronic plant radionuclide burden will account for less radioactivity entry into food chains, and attendant radiological hazards are low-level and of a long-term duration.

Results from field and laboratory experiments on fescue grass have been integrated with the aid of systems modeling techniques to illustrate relative concentrations of radiocesium in different ecosystem components following a unit source deposition in a fescue meadow. Initial conditions and transfer functions used in the model are summarized in Table 1.5. Radiocesium transfers among plant-litter-soil components were defined as linear and exponential functions (τ 's, Table 1.5), and the equations for change in state of six compartments were solved with a Runge-Kutta routine provided by Com-Share. Within limits, the results of this simulation (Fig. 1.3) fit observed concentrations and trends of radiocesium weathering in different components of a grass-soil system as a function of time

Fig. 1.3. Simulated concentrations of radiocesium in plant-soil segments of fescue grassland contaminated with fallout simulant particles. Initial deposit was partitioned between foliage and litter in the ratio 1:9.

14. H. L. Kriger et al., p. 59 in *Radiocological Contamination Processes*, B. Aberg and F. P. Hungate (eds.), 1966.

15. L. J. Middleton, *Int. J. Radiat. Biol.* 4, 387 (1959).

Table 1.5. Initial conditions and transfer functions used in the simulation of radiocesium dynamics in a fescue meadow

Compartment	Initial condition ^a	Functions of fractional transfer (τ) from specified compartment (day ⁻¹)		
		Definition	Form	Parameter
Foliage surface (E)	0.1	$\tau_1 = w_1 E$, particle weathering ^b	Negative exponential ($w_1 = e^{-\lambda t}$)	$X = 0.25$ $t = \text{day}$
		$\tau_2 = aq_1 E$, particle to leaf surface leaching ^c	Negative exponential ($a = e^{-\lambda t}$)	$\lambda = 1.34$ $q_1 = 0.15$ $t = \text{day}$
		$\tau_3 = c_1 E$, leaf turnover ^d	Constant linear	$c_1 = 0.006$
Litter (L)	0.9	$\tau_4 = c_2 L$, litter turnover ^d	Constant linear	$c_2 = 0.005$
Soil (S)	0.0008	$\tau_5 = c_3 S$, root uptake ^e	Constant linear	$c_3 = 0.0003$
Root (R)	0.0008	$\tau_6 = c_4 R$, translocation to foliage ^f	Constant linear	$a_4 = 0.004$
		$\tau_7 = c_5 R$, root excision, turnover ^g	Constant linear	$c_5 = 0.0007$
Foliage burden (B)	0.0002	$\tau_8 = w_2 B$, leaf death and weathering ^c	Negative exponential ($w_2 = e^{-\lambda t}$)	$\lambda = 0.02$ $t = \text{day}$
		$\tau_9 = f_1 q_2 B$, translocation to influence ^e	Exponential ($f_1 = (1 - e^{-\lambda t})$)	$\lambda = 0.02$ $t = \text{day}$
		$\tau_{10} = f_2 q_3 B$, translocation to root ^e	$f_2 = (1 - e^{-\lambda t})$	$\lambda = 0.02$ $t = \text{day}$ $q_3 = 0.02$
Influence (I)	0.0			

^aUnit input was initially partitioned between foliage surface and litter. Initial soil content was specified as 8×10^{-4} of total input; root content (8×10^{-4}) assumed to be equilibrated with soil; foliage burden specified as 0.2 of total plant content (1.6×10^{-3} , see footnote d). Influence functions as a sink and receives input from foliage burden (B).

^bR. C. Dahman, in *Survival of Food Crops and Livestock in the Event of Nuclear War*, AEC-CD CONF 700900 (in press).

^cR. C. Dahman et al., p. 153 in *Environmental Contamination by Radioactive Materials*, IAEA/STIPUB/226, 1970.

^dJ. M. Kelly et al., ORNL-4310 (1969).

^eR. C. Penhale et al., *Nature* 185, 707 (1960).

^fR. Handley et al., *Radlat. Bot.* 10, 577 (1970).

^gR. C. Dahman et al., *Ecology* 46, 84.

after contamination. This scenario illustrates redistribution following a single acute input, where foliage and litter retained 10 and 90% of the particle deposit, respectively. Results of the simulation also illustrated the highly dynamic nature of radiocesium during the initial two- to three-week period following contamination. Particle weathering, leaching, and intraplant movement of radiocesium are processes which accounted for dynamic redistribution initially, and, thereafter, radiocesium fluxes become less dynamic as new equilibria depended on uptake from the soil pool.

Experiments which provided data for this simulation focused on particle dynamics in litter and foliage,

plant-particle interactions, and radiocesium mobility in aboveground vegetation.¹⁶ Estimates of plant uptake from soil were based in part on other literature information. Data on radiocesium content of roots were incomplete, but the trend for root contamination was within an acceptable limit based on other reports of radiocesium root/shoot ratios.^{17,18} Simulated radi-

16. R. C. Dahman et al., p. 153 in *Environmental Contamination by Radioactive Materials*, IAEA/STIPUB/226, 1970.

17. R. C. Dahman, in *Survival of Food Crops and Livestock in the Event of Nuclear War*, AEC-CD CONF 700900 (in press).

18. R. Handley et al., *Radlat. Bot.* 10, 577 (1970).

cesium concentration trends in litter, soil, foliage, and fruit were accurate representations of observed redistribution in field and laboratory experiments. This was true for both trends of redistribution and relative magnitude of radiocesium in the different compartments as a function of time.

The importance of this simulation is to demonstrate relative concentrations of a nuclide in different components of the ecosystem following an acute contamination event. In this scenario, and apparently in others,¹⁹ the litter component initially retained the greatest fraction of radioactivity, and it also exhibited the slowest turnover time. After several months, this component still retained the largest fraction of the initial input. The radiocesium content of living foliage diminished rapidly, and one month later it approached a concentration level which was two orders of magnitude less than that at t_0 . Soil acted as a sink for the contaminant, but equivalent amounts in litter and soil did not occur until six months after contamination according to this simulation. An important ecological implication is that appreciable long-term retention in the litter component may lead to substantial concentrations in detrital-based food chains. Where dead organic material is an important dietary constituent, radionuclide ingestion would be at least two orders of magnitude greater than if living plant material constituted the food base. Empirical and simulation information on relative concentrations also would aid the design of ecological monitoring programs because it would identify segments of the system that have the highest hazard potential with regard to food chain reconcentrations and exposure of endemic organisms.

Direct Radionuclide Transfer from Canopy to Understory Vegetation

Mineral cycling studies between trees and understory vegetation have shown the importance of the leaching action of rainwater in tree canopies. The loss rate of leached substances from canopies and subsequent absorption by understory plants describes one mode of mineral transfer in nutrient cycles within terrestrial ecosystems. A persimmon (*Diospyros virginiana* L.) tree was tagged with 4.1 mCi of ^{134}Cs to study the pathways and rates of movement of ^{134}Cs leached from a tree canopy into understory vegetation. Rainfall and throughfall samples were collected immediately following rains for a period of eight weeks to determine total rainfall and amount of ^{134}Cs leached from the canopy. Understory vegetation, an almost pure stand of goldenrod (*Solidago canadensis* L.), was sampled

Table 1.6. Average ^{134}Cs content in understory plants (goldenrod) and soil under a tagged tree after eight weeks of leaching

Plant part	Foliar absorption (μCi)	Foliar + soil
Foliage	1830 $\pm$ 270	1759 $\pm$ 357
Stems	344 $\pm$ 71	369 $\pm$ 101
Roots	446 $\pm$ 80	909 $\pm$ 126
Total	2620	3037
Soil	47 $\pm$ 18	224 $\pm$ 68

weekly to determine uptake of ^{134}Cs by plants. Previous to inoculation, a plastic sheet was placed around each of 30 goldenrod plants to prevent vertical movement of ^{134}Cs into soil around these plants. This design enabled the determination of the extent of foliar vs root uptake of leached ^{134}Cs in throughfall.

Over an eight-week period 1.03% of the inoculum was leached from the tree canopy by 13 rain events totaling 10.9 in. About 0.04% (1.78 μCi) of the inoculum was transferred directly to understory plants. Table 1.6 shows the average ^{134}Cs content of goldenrod and soil under the tagged tree after eight weeks. Plants, which accumulated radiocesium through the foliar route only, contained 86% of the amount which was absorbed through both foliar and soil uptake pathways. These results indicate that nuclide transfer via rainout was approximately six times greater than root assimilation, and foliar absorption is a major pathway for radiocesium transfer from the canopy to understory vegetation.

Transpiration of ^3H by Deciduous Trees

Measurement of transpiration of water by trees is a difficult problem that has not been adequately resolved. Numerous methods have been attempted, but all are subject to criticism,²⁰ and tritiated water as a tracer represents a different approach to the measurement of transpiration based on theoretical tracer dynamics in steady-state systems.^{21,22} This method has been used successfully in tropical vegetation,²³ but not for temperate deciduous trees. A pilot study was undertaken to test the feasibility of using tritiated water to

19. A. S. Rogowski et al., *Health Phys.* 11, 1333 (1965).

20. R. O. Slayter, *Plant-Water Relationships*, Academic, New York, 1967, 366 pp.

21. P.-E. E. Bengtson, *Isotop. Radiat. Technol.* 3, 245-62 (1966).

22. K. Ljunggren, *Isotop. Radiat. Technol.* 5, 3-24 (1967).

23. J. R. Kline et al., *Ecology* 51, 1068-73 (1970).

measure rates of transpiration of temperate deciduous tree species under field conditions. The tree species examined in this study were yellow poplar (*Liriodendron tulipifera*) and shagbark hickory (*Carya ovata*).

The ^3H content of foliage was determined at various time intervals after tagging, and, according to previously developed analytical procedures,^{2,3,24} transpiration was estimated from

$$M = F \int_0^{\infty} f^1(t) dt,$$

where M is the total activity originally injected, F is the flow rate through the system (transpiration, in this case), and $f^1(t)$ is the specific activity of the tracer at the exit point (foliage) at any time following introduction of the tracer to the system.

Transpiration estimates for the period May 29 to April 9 are summarized in Table 1.7. The overstory yellow poplar had a transpiration rate per unit weight of foliage which was 1.5 times the rate for the hickory. Although canopy position was different, these transpiration estimates reflect the site requirements of the two species. While shagbark hickory usually competes successfully on more xeric sites than yellow poplar, the tagged trees were within 50 m of one another and likely were influenced by the same soil water regime. The understory yellow poplar lost water at a rate of 2.2 times that of the overstory yellow poplar and 3.2 times that of the hickory. Yellow poplar is known to have a low tolerance to canopy suppression, and often this is related to root competition for water or minerals and photosynthetic capacity of trees. The higher rate of

transpiration of the understory yellow poplar would deplete soil moisture more rapidly than for hickory, and extensive water utilization may lead to more rapid development of moisture stress during temporary summer droughts. Such experiments provide clues on comparative water relations in forests.

These preliminary results indicate the applicability of using tritiated water to make field estimates of transpiration in temperate deciduous trees. The technique provides an estimate of transpiration rate or total water loss for a period of 10 to 20 days. The method is best suited to species site comparisons where seasonal estimates of whole-tree water loss are required. Other in-progress studies such as vertical and lateral soil-water movement and the soil-water-plant transfer will enhance our understanding of the water cycle in forests. Since water is an important carrier of radionuclides in the terrestrial environment, accurate information on the dynamics of this cycle will aid the evaluation of radionuclide mobility in the landscape.

SOIL-PLANT RELATIONS

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Availability of radionuclides to ecological and human food chains over long time periods is influenced largely by plant uptake from soil. Through chemical sorption mechanisms, the soil typically functions as a sink as it effectively removes radioactive contamination from biotic circulation. Relative to vegetation contamination from direct foliar uptake, this mode of transfer results in concentrations diminished by at least several orders of magnitude. While biological hazards usually decrease accordingly, it is necessary to evaluate the significance

24. J. R. Kline et al., *Radionuclides in Ecosystems*, USAEC-CONF-710501 (in press).

Table 1.7. Preliminary transpiration estimates for temperate deciduous trees based on flux of a tritiated water stem tag. Eight 1-ml aliquots (0.591 $\text{m}^2\text{Ci/ml}$) were introduced to each tree on May 16, 1971.

Tree (d.b.h.)	Canopy position	Estimated foliage biomass ^a (kg)	Transpiration loss per day (liters)	Transpiration loss per kilogram of foliage per day (liters)
Yellow poplar (9.7 cm)	Overstory	4.85	124	30.6
Yellow poplar (10.7 cm)	Understory	1.85	120	65.9
Shagbark hickory (9.7 cm)	Understory	1.85	38	20.5

^aFoliage biomass estimated allometrically by $\hat{Y} = [-3.498 + 695 (\ln X)]^{1.36}$, where X = diameter breast height (cm) and $\hat{Y}$ = foliage biomass (kg).

of the long-term radionuclide burden in plants and animals which occurs as chronic uptake from soil. For the plant-soil (or root-soil) interface, research results are presented on the soil chemistry of radionuclides, the factors which influence radionuclide uptake by plants, and the reciprocal transfer of radioactivity from root to soil.

Redistribution of ^{137}Cs in Forest Soil

Distribution of ^{137}Cs within the soil profile and among soil fractions which were collected in 1962 and 1969 is presented in Fig. 1.4. The higher ^{137}Cs concentration in the 1962 soil sample at the 6-cm depth (about 2.1 pCi/mg), relative to that at the 4-cm depth (about 1.9 pCi/mg), was not observed in the 1969 samples. Furthermore, the data demonstrated ^{137}Cs movement through the soil profile, for example, approximately 12% of the soil burden in 1969 was below 10 cm while in 1962 less than 4% was at this depth. However, downward movement was quite slow (Fig. 1.4), because it took seven years for the radiocesium soil burden (3 pCi/mg) to move 3.6 cm (0.51 cm/year).

Fig. 1.4. ^{137}Cs soil concentration as a function of soil depth. 1969 values based on composite of 20 subsamples. 1962 values are from Waller and Olson [H. D. Waller and J. S. Olson, *Ecology* 48, 15-25 (1967)].

The ^{137}Cs buildup in the top 4 cm was attributed to radiocesium recycling processes such as flushing from the tree, litter input, and bidirectional redistribution from mixing by soil fauna.

Selective sorption by clay was examined for 1962 and 1969 samples where the radiocesium on clay was expressed relative to the percent clay (enrichment factor) as a function of increasing soil depth (Fig. 1.5a). At the soil depth of 6 cm this factor was much smaller in 1969 than in 1962, and the difference could have resulted from a loss of ^{137}Cs or an accumulation of clay. The percentage of clay determined at this depth in 1969 was approximately one-half that determined from the 1962 composite sample (1969 clay content = 5.5, and 1962 = 10.5% at a depth of 6 cm). While the discrepancy in clay content may be due to sampling variability, the data strongly indicated a loss of ^{137}Cs (from 1962 to 1969) at the 6-cm depth and a gain at lower depths relative to the clay present. Such redistri-

Fig. 1.5. Fraction of the total ^{137}Cs soil burden (<2 mm) in clay (a) and fine silt (b) relative to percentage of clay or silt as a function of depth in a forest soil. Enrichment factor = percent of total ^{137}Cs in clay/percent clay.

bution (6 to 20 cm in seven years) is unusual according to existing concepts of intensive sorption of cesium on clay. The data concerning the relative quantity of ^{137}Cs in the fine silt fraction are presented in Fig. 1.5b in terms of enrichment factor as a function of depth. In this case, the 1962 relationship was nearly inverse to what it was for clay. Over seven years there was a tendency for amounts of ^{137}Cs to be transferred from the clay to fine silt. Cesium-137 concentration in the fine silt (1.54 pCi/mg) at the 12- to 16-cm depth was nearly equal to that found in the clay (1.85 pCi/mg). Furthermore, over one-third of the total ^{137}Cs soil burden was found in the silt fraction at this depth. Long-term observation of ^{137}Cs behavior in forest soil indicates considerable redistribution between soil separates as well as throughout the profile. Although availability to associated biotic components has diminished to new equilibria, the dynamic state of radio-cesium in the soil component of this ecosystem merits observation in long-term assessments of low-level radiological hazard.

Plant Uptake of Radionuclides from White Oak Lake Bed Soil

The amount of radionuclide transferred from soil to plant, and subsequently through several animal food chains, is being determined by using a highly contaminated soil. The first portion of the experiment involves the evaluation of various parameters which influence transfer of the radionuclide from the soil to the plant. One of the most important environmental variables which influences radionuclide uptake by plants is the nutrient status of the contaminated soil, and a factorial N-P-K fertilization experiment (three levels of the following essential elements: N—0, 50, 100 ppm; P—0, 25, 50 ppm; K—0, 75, 150 ppm replicated three times) was designed to determine the effect of nutrient level on uptake by plants from White Oak Lake bed soil.

The first harvest and radioassay of radionuclides taken up by Japanese Millet grown in the greenhouse in a soil from the environs of White Oak Lake has been completed. Data from the N-P-K fertilization experiment indicated that phosphorus application enhanced the uptake of ^{60}Co and ^{137}Cs . Applications of potassium reduced the plant uptake of ^{137}Cs , showing the competitive effect of a nutrient analog. High applications of nitrogen also reduced ^{137}Cs uptake and, in a general sense, such relationships among the monovalent cations would be expected since the nitrogen was added in the form of urea, and NH_4^+ , K^+ , and Cs^+ have similar cationic radii. This uptake experiment

Table 1.8. Radionuclides present in White Oak Lake soil prior to planting Japanese Millet

Radioactivity (pCi/g soil dry weight)

^{106}Ru	^{137}Cs	^{60}Co	^{125}Sb	^{65}Zn	^{90}Sr
2.7	2.2	13.6	1.4	0.2	0.014

will continue for five or six harvests to ascertain long-term uptake under exhaustive cropping conditions.

Only the radionuclides ^{137}Cs and ^{60}Co were present in significant quantities in the first crop of millet grown in White Oak Lake soil (Table 1.8). The fertilizer treatment which gave the highest ^{60}Co content in plant tissue (180 pCi/g) corresponded to a concentration factor (pCi/g in dry plant/pCi/g in dry soil) of 0.0132.²⁵ The ^{137}Cs plant concentration varied from 50 to 90 pCi/g and resulted in a concentration factor of approximately 0.0318. This value is similar to that reported by Menzel²⁶ but the concentration factor of ^{60}Co was considerably lower. His data reflected only plant uptake within six months after a water-soluble source was applied directly to the soil, whereas contaminants in WOL soil have been influenced by long-term secondary soil reactions. Preliminary results on plant uptake of ^{137}Cs and ^{60}Co from soil which was contaminated 10 to 20 years earlier indicate that discrimination between plant and soil may increase with time, and magnitudes of transfer to plants diminish accordingly. Fixation of the nuclides in secondary reaction products is the proposed mechanism which decreases radionuclide availability.

Transfer of Radiocesium from Root to Soil

Prior research²⁷ has shown the root to soil pathway to be an important transfer mechanism by which radiocesium moves from aboveground vegetation to the soil sink. Rapid root turnover may account for movement from plant to soil, and a ^{134}Cs tracer was used to estimate transfer rates to three different soils (Talbott silty clay, Sequatchie sandy loam, and Esory silt loam) due to root processes such as exudation, leaching, and death and decay. The investigation also was designed to eliminate mineral contribution to the soil pool from leaching of aboveground vegetation.

25. Value of <1.0 is regarded as a discrimination factor because dilution rather than concentration characterizes the transfer process.

26. R. G. Menzel, *Health Phys.* 11, 1325-32 (1965).

27. J. S. Olson, *J. Ecol.* 52 (Suppl.), 99 (1964).

Seedlings harvested one week following stem tagging with ^{134}Cs had significant quantities of this radionuclide in the root and soil compartments. The greatest percentage of the total budget was in the old stem and leaves, but from 6 to 30% had moved down into the roots during the seven-day period. Based on calculations of dry weight percentages in five root compartments (four size classes and dead roots), root size classes contained a disproportionate amount of total seedling dry weight. However, the smaller root size classes contained nearly three times more radiocesium than other size classes (Table 1.9). Dead roots had the lowest radioactivity per unit of dry weight of any of the seedling compartments, which was attributed in part to increased susceptibility to leaching following root death. Examination of soil indicated as much as 3% of the total ^{134}Cs was in this compartment after only seven days. Most of the initial transfer to soil probably was due to root death, decay, or leaching from living roots since exudation likely was negligible during the early time interval. These observations confirm prompt transfer of radiocesium between shoots and roots when radiocesium is assimilated by aboveground plant parts.

Table 1.9. Concentration ($\mu\text{Ci/g}$) of ^{134}Cs in *Liriodendron* roots one week after labeling shoots

Root classes ^a	NM ^b	ME ^c
Talbot silty clay		
1	0.0	0.0
2	0.3823 $\pm$ 0.30	0.3659 $\pm$ 0.25
3	1.3191 $\pm$ 0.86	0.9893 $\pm$ 0.66
4	3.3570 $\pm$ 1.85	1.5902 $\pm$ 0.88
5	0.0751 $\pm$ 0.01	0.1214 $\pm$ 0.07
Sequatric sandy loam		
1	0.0	0.0
2	0.3458 $\pm$ 0.14	0.5925 $\pm$ 0.08
3	0.5606 $\pm$ 0.14	1.1744 $\pm$ 0.31
4	0.2460 $\pm$ 0.20	2.7055 $\pm$ 0.68
5	0.0563 $\pm$ 0.03	0.2224 $\pm$ 0.04
Emory silt loam		
1	0.2289	0.0555
2	0.7744 $\pm$ 0.05	0.9828 $\pm$ 0.52
3	1.5156 $\pm$ 0.117	1.7050 $\pm$ 0.76
4	3.7844 $\pm$ 0.75	2.9591 $\pm$ 1.46
5	0.0980 $\pm$ 0.01	0.3317 $\pm$ 0.15

^aRoot diameter classes: 1, >1.0 cm; 2, 1.0 to 0.5 cm; 3, 0.5 to 0.1 cm; 4, <0.1 cm; 5, dead roots.

^bNM, canopy minerals leached to soil.

^cME, mineral leaching to soil prevented.

A continuation of these investigations will partition radiocesium and mineral turnover among exudation, leaching, and root death-decay processes.

Distribution of ^{137}Cs between Montmorillonite and Mica Minerals

Selective adsorption of ^{137}Cs to micaceous minerals is so great in comparison with other clay minerals that most of the ^{137}Cs in soil should ultimately be associated with the micaceous component, providing the soil contains this mineral.²⁸ Rapidity of fixation in mixed clays is an important process because the fixation rate would influence downward penetration of ^{137}Cs , and in a soil horizon containing a mixture of a large amount of montmorillonitic clay (nonspecific cation exchange sites) and only a small quantity of mica, the latter mineral may selectively sorb the cesium. Through the use of ultrazonal centrifugation, montmorillonite and mica minerals (less than 2 μ diam) can be quantitatively separated from suspensions of two clays, and exchanges of ^{137}Cs between montmorillonite and mica can be detected through the isolation of each mineral from a suspension containing ^{137}Cs by determining the fraction of ^{137}Cs associated with each mineral for different time intervals.

Fifty mg of each mineral (<2 μ) was suspended in 10 ml of 1 N MgCl_2 containing tracer quantities of ^{137}Cs , and the suspensions were separated by centrifuging through a density gradient at 15 min and 24- and 72-hr intervals.²⁹ Three bands were removed: band 1 was less than 2.3 g/cm³ in density, band 2 consisted of dispersed material between the two dominant bands (density 2.3 to 2.6 g/cm³), and band 3 was greater than 2.6 g/cm³ in density. X-ray diffractograms showed that band 1 was montmorillonite, while bands 2 and 3 contained mica (the 1.0-nm maximum in band 3 was much more pronounced than that in band 2). No montmorillonite could be detected in bands 2 and 3. Mica from soil clays characteristically bands in the density range 2.62 to 2.75 g/cm³.

Results on radioactivity retention by the different banding fractions (Table 1.10) showed essentially no transfer of ^{137}Cs from the nonspecific exchange sites (montmorillonite) to the micaceous fraction over the 72-hr interval. Lower radiocesium content of all band fractions at $t + 15$ min indicated incomplete sorption to

28. T. Tamura et al., *Health Phys.* 2, 391 (1960).

29. C. W. Francis et al., "An Evaluation of Zonal Centrifugation as a Research Tool in Soil Science. Part 1: Methodology," accepted for publication in *Am. Proc. Soil Sci.*

Table 1.10. Adsorptive distribution of ^{137}Cs between montmorillonite and mica minerals after zonal centrifugation^a

Band	Clay mineral	Bandweight (mg)	^{137}Cs Activity		
			Percent	nCi/mg	Relative to band 1
15 min					
1	Mt ^b	55.0 ± 1.9 ^c	7.9	2.8 ± 0.2	1.0
2	Mica	30.5 ± 0.3	69.1	24.6 ± 0.4	8.8
3	Mica	15.5 ± 0.3	23.0	8.2 ± 0.4	2.9
24 hr					
1	Mt	59.0 ± 0.7	10.8	5.5 ± 0.1	1.0
2	Mica	24.6 ± 0.8	65.7	33.5 ± 0.4	6.1
3	Mica	17.1 ± 0.1	23.5	12.0 ± 0.2	2.2
72 hr					
1	Mt	60.7 ± 1.0	8.1	4.1 ± 0.1	1.0
2	Mica	25.1 ± 0.1	68.4	34.5 ± 0.3	7.8
3	Mica	18.7 ± 1.0	23.4	11.8 ± 0.7	2.9

^aBands were separated from a suspension of 50 mg each of <2 μ of montmorillonite and mica in 1M MgCl_2 .

^bMt = Montmorillonite.

^cMean value of two replications; plus or minus refers to range of absolute value.

both montmorillonite and mica. From t_{24} to t_{72} hr, small but insignificant decreased sorption on montmorillonite and increased sorption on mica were observed. In general, less than 10% of the total adsorbed activity was associated with the montmorillonite clay while the bulk of the activity (60 to 70%) initially was adsorbed to the light-density (2.3 to 2.6 g/cm^2) micaceous fraction.

The large fraction of the mica which was found at densities less than 2.6 g/cm^3 (greater than 60%) was somewhat surprising. The material was banded in an ultracentrifuge at 15,000 rpm (38,500 g at r_{max}) for 17 hr which normally is a sufficient force to band, isopycnicly, clay particles as small as 0.05 μ in diameter. Further sedimentation studies on the mineral stock showed that the mica had a particle size distribution where over 75% was in the 2.0- to 0.2- μ range, and the fraction less than 0.05 μ was considerably smaller than the 60% which was isolated in band 2. Thus, material in band 2 was at its true isopycnic point and possessed different characteristics from that banded at densities greater than 2.60 g/cm^3 . Determination of potassium content of the bands (5.64 and 7.96% for bands 2 and 3, respectively) revealed that band 2 was more weathered and consequently more susceptible to

hydration and solvation than band 3. It was this band which had three to four times more ^{137}Cs sorption capacity than the less-weathered crystalline mica, and conceivably this material contained a larger number of wedge sites.³⁰ This condition would optimize interlayer spacing and selective ^{137}Cs adsorption between the 1.0 and 1.4 rather than 1.0-nm lattice spacing.

Plutonium Plant-Soil Relationships

One result from implementation of the fast breeder reactors will be the increased production of plutonium. The projected cumulation of plutonium isotopes from the United States nuclear power industry alone is over 1000 megacuries (per year) by the year 2020.³¹ This large increase in production may also increase the probability of plutonium releases to the environment. Expected magnitude of Pu uptake by plants has been summarized from a review of plutonium relationships in vegetation-soil systems.³²

Plutonium in soil exists largely in a positively charged polymeric form and is strongly adsorbed to colloids. Aqueous solutions of inorganic salts have removed little plutonium after initial adsorption (<4%); however, acetate salts inhibited plutonium adsorption to soil and also have extracted large quantities of adsorbed plutonium. Likewise, plutonium in the presence of various organic solvents was not sorbed to soil particles. It appears plutonium movement in soils is very limited unless it becomes associated with certain synthetic or naturally occurring organic compounds.

Plutonium uptake by plants is apparently similarly related, for example, the discrimination factor of plutonium transfer from soils to plants is generally in the order of 10^{-4} to 10^{-6} (concentration in plants to concentration in soils) (Table 1.11). However, Romney et al.³³ demonstrated enhancement of ^{239}Pu uptake in alfalfa as much as tenfold through the addition of a chelating agent (diethylenetriaminepentaacetic acid). By necessity, many experiments have involved modified or artificial growth media, and there is limited information on potential chelation effects from organic rich soils.

30. D. L. Dolcater et al., *Soil Sci. Soc. Amer. Proc.* 32, 795 (1968).

31. D. G. Jacobs and Ferruccio Gem, *Health Phys. Div. Annu. Prog. Rep. July 31, 1969*, ORNL-4446, pp. 17-20.

32. C. W. Francis, "Plutonium Mobility in Soil and Uptake in Plants: A Review," submitted to *Journal of Environmental Quality*.

33. E. M. Romney, H. M. Mork, and K. H. Larson, *Health Phys.* 19, 487-91 (1970).

Table 1.11. Fraction of plutonium uptake by various plants grown under different conditions

Growth conditions	Plant	Fraction assimilated from soil	Reference
Nutrient-bentonite suspensions	Barley	$(1.0-0.04) \times 10^{-2}$	<i>a</i>
Neubauer	Oat	$(0.1-0.01) \times 10^{-2}$	<i>b</i>
Soil-modified Neubauer	Barley	$(0.02-0.006) \times 10^{-2}$	<i>c</i>
Soil-greenhouse	Ryegrass	10^{-4}	<i>d</i>
Soil-greenhouse	Oat	$(0.02-0.001) 10^{-2}$	<i>e</i>
Soil*-greenhouse	Clover	2.5×10^{-6} (1958) 8.8×10^{-5} (1962)	<i>f</i>

^aLouis Jacobson and Roy Overstreet, *Soil Sci.* 65, 129-34 (1948).

^bJ. H. Rediske, J. F. Cline, and A. A. Selders, USAEC Report HW-36734, 1955.

^cD. O. Wilson and J. F. Cline, *Nature* 209, 941-42 (1966).

^dP. Newbould, p. 86 in *Annual Report on Radiobiology*, ARCL10, Great Britain Agricultural Research Council, Radiobiological Lab., Woburn, Berks, England.

^eS. L. Cummings and L. Bankert, 1971, *Radiat. Health Data Rep.* 12, 83-85 (1971).

^fE. M. Romney, H. M. Mork, and K. H. Larson, *Health Phys.* 19, 487-91 (1970).

*Soil from Nevada Test Site.

A joint project between the Radiation Waste Disposal Section of the Health Physics and Ecological Sciences Divisions is being carried out on the chemical characterization of plutonium adsorbed to soil from the Nevada Test Site area. In addition to conventional soil extraction procedures, the soil samples will be segregated by ultrazonal centrifugation techniques. Through such an approach specific reaction products in these soils should be isolated.

Ultrazonal Centrifugation Techniques

Successful evaluation of material transfers in ecosystems requires analytical techniques which can measure processes within the system. Over the past several years a technique has been developed which will segregate environment particulates on the basis of density. This is carried out through centrifugation of the material across density gradients (ultrazonal centrifugation). Methodology and results of this development are presented elsewhere,^{34,35} and additional research has been done on the interactions between dispersants and clays.

During the adaptation of ultrazonal centrifugation to environmental samples it became apparent that quantities of the dispersant (polyvinylpyrrolidone, PVP) used to maintain clay suspensions in the nonaqueous density gradients were being adsorbed to the clays. Adsorption

and desorption studies of PVP were made on three representative clay minerals (illite, bentonite, and kaolinite). Using gravimetric procedures, it was concluded that essentially all of the PVP adsorbed to illitic and kaolinitic clays can be desorbed by washings of H₂O or ethanol. However, in the case of bentonites, 10 to 14 g of PVP per 100 g of clay remained adsorbed after as many as six washings in H₂O or ethanol. Maximum adsorption of PVP was found to be in aqueous systems where the clay contained 85 to 90 g of PVP per 100 g of mineral.

Results of adsorption of PVP on Wyoming bentonite (API 26) at different temperatures and cation saturation from two solvents, water and 200 proof ethanol, are given in Fig. 1.6. These adsorption curves indicate monolayer coverage in the case of magnesium clay and double layer adsorption on the sodium-saturated bentonite; x-ray data supported this relationship.³⁶ To

34. C. W. Francis et al., "An Evaluation of Zonal Centrifugation as a Research Tool in Soil Science. Part I: Methodology," accepted for publication in *Soil Sci. Soc. Amer. Proc.* (1971).

35. C. W. Francis et al., "An Evaluation of Zonal Centrifugation as a Research Tool in Soil Science. Part II: Characterization of Clays," accepted for publication in *Soil Sci. Soc. Amer. Proc.* (1971).

36. C. W. Francis, "Adsorption of Polyvinylpyrrolidone on Reference Clay Minerals," submitted to *Soil Science*.

evaluate the adsorption mechanism responsible for the apparently irreversible adsorption of PVP to bentonites, the adsorption data over different temperatures and concentrations were plotted as Langmuir and Freundlich isotherms (Fig. 1.7).

Adsorption data of PVP on Wyoming bentonite did not result in linear plots in the form of Langmuir adsorption isotherms. The graph gave a linear relationship when plotted as a Freundlich isotherm (Fig. 1.7);

$$x = kc^n,$$

where x is the amount of PVP adsorbed by unit mass of clay, c is the equilibrium solution concentration, and k and n are constants. The "isosteric" heat of adsorption

Fig. 1.6. Adsorption of PVP on Wyoming bentonite (W.B.).

Fig. 1.7. Freundlich adsorption isotherm - PVP on Wyoming bentonite.

was determined from equilibrium adsorption at two different temperatures. For the same amount of polymer adsorption at temperatures T_1 and T_2 , H was calculated from

$$\ln \frac{C_1}{C_2} = \frac{\Delta H}{R} \left(\frac{1}{T_1} - \frac{1}{T_2} \right),$$

where C_1 and C_2 are equilibrium solution concentrations at the respective temperatures. The isosteric heat of adsorption for 50 and 6 g of adsorbed PVP per 100 g of clay resulted in ΔH values of 6.34 and 6.47 kcal/mole, respectively. The magnitude and sign are similar to the heats of adsorption calculated in the same manner for the adsorption of polyvinylacetate on iron powder,³⁷ and the low values are indicative of physical adsorption rather than chemisorption. The proposed mechanism of adsorption of PVP on clay is the alignment of alternate carbon bonding in the polymer chain to exposed oxygen atoms in the hexagonal surface of layer silicates. The distance between the alternate carbon atoms (0.252 nm) closely approximates the distance between surface oxygen atoms in a unit cell of montmorillonite (0.259 nm). This type of adsorption would require all polymer segments to be adsorbable and all surface sites to be adsorbing, which results, according to Silberberg,³⁸ in a monolayer which would exhibit considerably less coiling and buckling than was previously conceived.

FOOD CHAIN DYNAMICS OF RADIONUCLIDES

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Food chains are the major biological process for environmental transport of contaminants and may yield either a concentration or dilution of materials from trophic exchanges. Much of the problem in establishing safe limits or standards for pollutants is that information on transfers of these pollutants from the abiotic environment to the biota is either insufficient or unavailable. Therefore, in most cases maximizing assumptions are invoked about transfer rates in food

37. J. R. Koral, *J. Phys. Chem.* 62, 541 (1958).

38. A. Silberberg, *J. Phys. Chem.* 66, 1884 (1962).

chains leading to man. However, concentration factors may be expected to decrease, not increase, from the nonliving to living parts of the ecosystem and from one link in the food chain to another. It becomes essential, then, that refined values are obtained for pollutant transfer rates among nonliving and living components of the ecosystem. In the following discussions, research is described on some of the numerous food chain parameters and environmental variables affecting transfer rates and concentration factors for these pollutant materials.

Through study of the variables affecting the dynamic food chain process, factors affecting the food chain dynamics of materials and, ultimately, their long-term fate in the biota can be better understood. Potential movement of materials throughout the biota of natural ecosystems involves innumerable variables such as dietary levels in the food, physiological state of the consumer, ingestion rates, whole-body chemistry, biological degradation, and turnover or excretion rates. Consequently, cause and effect relationships among these parameters are such that specific values are applicable only in the situation of the particular food chain being examined.

Factors Affecting Equilibrium of Radionuclides in Arthropods

Whole-body concentrations of chemical compounds in animals are the result of a combination of physiological and environmental variables. These variables affect the parameters of biological uptake and turnover of the chemical compounds and the environmental concentration of the compounds. Variations in any one of these parameters may produce marked differences in whole-body concentrations in the animals, with subsequent differences in concentration becoming apparent in the entire trophic level.

Biological uptake of radionuclides by arthropods often has been described as a double exponential system composed of a fraction of the ingested material which passes through the gut (p_1) and a fraction which is assimilated into body tissues (p_2). This model of radioisotope uptake is depicted mathematically as

$$Q_t = Q_e - p_1 Q_e e^{-\lambda_1 t} - p_2 Q_e e^{-\lambda_2 t}, \quad (1)$$

where Q_t = whole-body concentration of radioisotopes at time t , Q_e = the equilibrium whole-body concentration of radioisotopes, λ_1 = an estimate of the rate of gut passage ($p_1 Q_e$), and λ_2 = an estimate of the turnover rate of assimilated radioisotopes ($p_2 Q_e$).

Differences in turnover coefficients between various chemical compounds or different species can significantly affect the time required for reaching equilibrium. The curves shown in Figs. 1.8 and 1.9 were derived from Eq. (1) by varying the values of λ_1 in five equal intervals between 0.032 and 0.096 and λ_2 in five equal intervals between 0.006 and 0.018 for two different equilibrium levels ($Q_e = 260$ and 130 dpm/mg for Figs. 1.8 and 1.9, respectively). These two families of curves

Fig. 1.8. Radioisotope uptake patterns for an equilibrium whole-body radioactivity content (Q_e) of 260 dpm/mg derived from an assimilation value (p_2) of 0.66 with respective combinations of turnover rates λ_1 and λ_2 (0.032, 0.006), (0.048, 0.009), (0.064, 0.012), (0.080, 0.015), and (0.096, 0.018).

Fig. 1.9. Radioisotope uptake patterns for an equilibrium whole-body radioactivity content (Q_e) of 130 dpm/mg derived from an assimilation value (p_2) of 0.66 with respective combinations of turnover rates λ_1 and λ_2 (0.032, 0.006), (0.048, 0.009), (0.064, 0.012), (0.080, 0.015), and (0.096, 0.018).

serve to illustrate how variations in the biological elimination coefficients for unassimilated and assimilated fractions affect the biological uptake of elemental materials. For a given equilibrium level (Q_e), various environmental stresses on biological elimination rates (e.g., temperature) tend to either increase or decrease the time required to reach this equilibrium value. For example, in Fig. 1.8 only 300 hr are required to reach Q_e when $\lambda_1 = 0.096$ and $\lambda_2 = 0.018$, whereas Q_e is not reached even after 500 hr when λ_1 and λ_2 are decreased to 0.032 and 0.006, respectively. The diminished λ 's could conceivably be caused by a reduction in environmental temperature. The effect remains constant, for a given stress, even as the value of Q_e changes (Fig. 1.9) due to either fluctuations in environmental concentration of the radioisotope in question (biologically indeterminant equilibrium) or due to some change in the physiological requirements of the animal for the element (biologically determinant equilibrium).

Although various environmental and physiological variables affect the rates of uptake and turnover of materials, ultimate concentration factors for chemical compounds or elements are intimately related to the stable-element chemistry of the consumer organism and its food. Careful distinction should be made between elemental concentrations in organisms (ppm) and concentration factors for these elements in a food chain (ratio of ppm in organism to ppm in food).

Some organisms show relatively constant whole-body elemental compositions over a range of elemental concentrations in their environment. Under these circumstances, the elemental concentration factors are said to be *biologically determinant*, for example, biologically constant and inversely proportional to increased concentrations of the respective elements in the environment. Many nutrient elements active in metabolic processes appear to be biologically determinant. No significant seasonal differences in the sodium, potassium, and calcium content of grassland arthropods have been observed, although these elements varied through time in the grass food base. Similar relationships, although not without exceptions, have been reported for Na, K, and Ca in forest arthropod food chains. Organisms in food chains may concentrate these elements above levels in their food base, but once optimum whole-body concentrations are attained they remain constant despite subsequent fluctuation levels in their food.

Conversely, other classes of chemical compounds and elements have whole-body concentrations directly proportional to environmental concentrations. Elements which behave in this manner are *biologically indeterminant*.

Such elements are often those which are not metabolically active, and uptake and excretion by the animal follow simple mass balance equilibria. The behavior of ^{137}Cs in arthropod food chains (Fig. 1.10) illustrates this point. Whole-body concentrations of ^{137}Cs are directly proportional to levels in food, even though total cesium concentrations in various diet items were essentially constant. These data were derived from foliage-feeding insects, although similar relationships can be shown for detritus feeders and predators. Other such compounds are those for which the organism does not possess the capability for biological degradation and excretion, with resulting accumulation in certain body tissues. Although some environmental pollutants such as DDT and toxic heavy metals may be metabolized and excreted by the organism, their concentration appears biologically indeterminant.

^{137}Cs turnover in forest canopy aphids. The ^{137}Cs -tagged *Liriodendron* forest has been the subject of many studies of element cycling and food chain dynamics. These studies have followed the movement of cesium within trees and transfer to litter and soil layers, within litter, soil, and microorganism components, through forest floor food chains, and through several components of the forest canopy arthropod community. To date, forest canopy arthropod studies have emphasized population dynamics and energy flow in entire trophic levels. The results presented here will

Fig. 1.10. Linear relationship between concentration of ^{137}Cs in food and resultant equilibrium body burdens in foliage-feeding insects.

provide additional specific information on a major component (sap-feeding insects) of the forest canopy arthropod community – the aphid (*Macrosiphum liriodendroni*).

Preliminary data on biomass and density levels of this species coupled with information on metabolism, growth and reproduction, and honeydew production indicated that even at low biomass levels (<0.01 mg dry weight per cm² of leaf surface), *Macrosiphum* was an important component of the canopy community. Its high turnover rates of carbon (energy) and minerals contributed a significant input to the forest floor. The results presented here summarize the dynamics of ¹³⁷Cs movement through the aphid population.

Biological turnover rates of radiocesium in *Macrosiphum* were determined for the alate, subalate, and immature forms at temperatures of 15, 20, and 25°C. The resulting elimination data were fitted to the nonlinear model

$$A_t = A_0 e^{-\lambda t}, \quad (2)$$

with A_t = the ¹³⁴Cs activity at time t , A_0 = the initial ¹³⁴Cs activity, and λ = the ¹³⁴Cs turnover rate coefficient, and are shown in Fig. 1.11. Values of the biological turnover rate at each of the three experimental temperatures are shown in Table 1.12. Combined instar data were pooled for determining the slope values (λ) at each temperature for the curves shown in Fig. 1.11.

The effect of temperature on the biological turnover rate was analyzed in the equation

$$\lambda = \alpha e^{\beta (\text{temp in } ^\circ\text{C})}, \quad (3)$$

where α = an empirical constant derived during solution of the equation and β = the rate at which the biological

turnover coefficient changes with temperature. The results of this analysis are shown in Fig. 1.12 with a value of $\beta = 0.0488$. This resulted in a Q_{10} value of 1.63 which was not significantly different from a $Q_{10} = 2$ ($F < 0.05$), indicating that a twofold change in the

Fig. 1.11. Retention of ¹³⁴Cs in canopy aphids, *Macrosiphum liriodendroni*, following 24 hr of feeding on radiocesium-tagged *Liriodendron* leaves exposed as a function of temperature for three different aphid life stages.

Table 1.12. Turnover rates (hr⁻¹) of ¹³⁴Cs in different life stages of the *Liriodendron* aphid, *Macrosiphum*, expressed as a function of temperature

No significant differences ($P < 0.05$) were detected between any pairs of turnover rate values.

Temperature (°C)	Life stage					
	I + II	III	IV	Alate	Subalate	All
15	a	a	a	0.0504	0.0423	a
20	0.0523	0.0674	0.0474	0.0586	0.0542	a
25	a	a	a	0.0779	0.0661	0.0740

a Not determined.

Fig. 1.12. Relationship of the ^{134}Cs elimination rate for three life stages of the aphid, *Macrosiphum liriodendron*, to temperature.

rate of ^{134}Cs excretion will accompany a 10°C change in temperature within the animals' optimum temperature range.

Mean ^{137}Cs concentrations in *Liriodendron* leaves and plant sap from the forest were 2.6 ± 0.2 and 9.6 ± 0.8 pCi/mg dry weight, respectively. During the month of July (mean canopy temperature = 20°C), the equilibrium body burden of ^{137}Cs in the aphid population was 1.8 pCi/mg dry weight. The concentration factor for ^{137}Cs in *Macrosiphum* relative to leaves was 0.68, whereas relative to leaf sap it was only 0.18. The ingestion rate of ^{137}Cs by the aphid population may be calculated from

$$I = \lambda Q_e \quad (4)$$

Referring to Fig. 1.12, a mean turnover rate for ^{134}Cs at 20°C was determined to be 0.0565/hr. This estimate yielded a value of 2.441 pCi of ^{137}Cs ingested per mg animal per day, which represents 135% of the aphid equilibrium body burden per day. For an aphid population of mean body weight of 0.1 mg dry weight, honeydew production would account for a daily input of 0.5 pCi/mg of honeydew to the forest floor. Depending on the duration of peak population, this mode of transfer could account for significant and rapid transport of foliar materials to other segments of the ecosystem.

Food chain dynamics of tritium. Tritium is a radioactive waste product which may be released to the environment from reactor or fuel reprocessing opera-

tions. It is a beta emitter with a physical half-life of 12.3 years, is biologically active, and, once released to the environment, reacts with oxygen to form tritiated water (HTO) which may become incorporated into hydrocarbon molecules. These hydrocarbon molecules have been detected in seven of the glycolytic reactions in mammals. In spite of the wealth of information on sources and sinks of tritium in the environment, very little is known of the biological pathways and fluxes of ^3H as it moves through various ecosystem components. To provide some insight into the dynamics of tritium movement through a simple terrestrial food chain, laboratory experiments were initiated in which parameters of uptake and elimination of tritium were determined for crickets (*Acheta*) feeding on watercress leaves (*Nasturtium*) grown in an $0.5\text{-}\mu\text{Ci } ^3\text{H/ml}$ nutrient solution. Equilibrium concentrations of tritium in watercress leaves during uptake experiments were 119.8 ± 42.8 pCi/mg for fresh material and 42.8 ± 7.2 pCi/mg for material which was dried prior to the oxidation step of sample preparation.

Whole-body concentrations of tritium in fresh crickets were plotted as a function of time with the resulting curve (Fig. 1.13) based on the model

$$Q_t = Q_e(1 - e^{-\lambda t}) \quad (5)$$

where Q_t is the whole-body concentration of tritium at time t , Q_e is the whole-body equilibrium concentration of tritium, and λ is the rate coefficient for whole-body tritium uptake. The time required to reach an equilibrium concentration (Q_e) of 49.7 dpm/mg was eight days. The uptake rate coefficient (λ) for whole-body tritium was 0.456/day. Tissue-bound tritium concentrations as determined from dried samples were also analyzed with the nonlinear model [Eq. (5)] and are shown in Fig. 1.13. In this instance, ten days were required to reach Q_e (8.4 dpm/mg). The uptake rate coefficient (λ) for tissue-bound tritium was 0.288/day.

Once a best least-squares fit was obtained for both the whole-body and the tissue-bound fractions, the resulting curves were subtracted geometrically (whole body minus tissue bound) to obtain a predicted curve for body-water tritium concentrations (dashed line of Fig. 1.13). Equation (5) was utilized with the data for body-water tritium concentrations to obtain estimates of body-water equilibrium concentration (41.8 dpm/mg) and the body-water tritium uptake rate coefficient ($\lambda = 0.480/\text{day}$).

These results suggest that the body-water compartment accumulates ingested tritium (which was in ionic and organic form) at approximately twice the rate of

Fig. 1.13. Patterns of tritium uptake in *Acheta* for body-water, tissue-bound, and whole-body components while feeding on tritium-tagged watercress.

the tissue-bound component. However, no attempt was made to distinguish between ionic and organic forms of tritium in the tissue-bound compartment. At equilibrium, 17% of the ingested tritium was in the tissue-bound compartment. A concentration factor of 0.42 was determined for the ratio of whole-body tritium concentration in the cricket to the tritium concentration in fresh plant material. For the tissue-bound compartments of both watercress and crickets, this ratio was only 0.20, indicating that the food chain transfer of metabolically fixed tritium was somewhat less efficient than that of whole body, in which case the body-water compartment predominates.

Tritium elimination was also determined by feeding tagged watercress leaves (180.2 ± 64.4 pCi/mg for fresh material and 18.5 ± 3.1 pCi/mg for material dried prior to oxidation) to crickets for 24 hr. Whole-body and tissue-bound tritium were determined upon termination of feeding, and elimination data were fitted to a two-component model (gut contents and material actu-

ally assimilated into the body), depicted mathematically as

$$A_t = A_0 (p_1 e^{-\lambda_1 t} + p_2 e^{-\lambda_2 t}), \quad (6)$$

where A_t is the tritium concentration at time t , A_0 is the initial tritium concentration, p_1 and p_2 are proportionality constants for gut (p_1) and body tissue (p_2) components, and λ_1 and λ_2 are the loss-rate coefficients associated with the gut (λ_1) and body tissue (λ_2) components.

Initial whole-body tritium concentration following 24 hr of feeding was 50.5 dpm/mg (Fig. 1.14). Parameter values for tritium elimination [Eq. (6)] of p_1 and p_2 were 0.27 and 0.73, respectively, and λ_1 and λ_2 were 8.158 and 0.173/day, respectively. Least-squares fitting of the tissue-bound tritium concentrations through time resulted in the following: $A_0 = 9.8$ dpm/mg, $p_1 = 0.28$, $p_2 = 0.72$, $\lambda_1 = 8.158$ /day, and $\lambda_2 = 0.072$ /day. Geometric subtraction of the tissue-bound curve from the whole-body curve resulted in a predicted curve depicting tritium loss from the body-water compartment (dashed line of Fig. 1.14). Data derived for the body-water compartment were fitted with Eq. (6), and the following parameter values were obtained: $A_0 = 45.2$ dpm/mg, $p_1 = 0.32$, $p_2 = 0.68$, $\lambda_1 = 20.397$ /day, and $\lambda_2 = 0.221$ /day.

Elimination of tritium contained in the liquid fraction of the gut contents was three times more rapid than elimination of tritium from the solid fraction. This ratio of 3:1 also held for tritium elimination from assimilated material, that is, body-water tritium elimination was three times more rapid than tissue-bound tritium. Assimilation of ingested tritium was approximately the same for body-water and tissue-bound compartments. Tissue-bound (ionic and organic) tritium accounted for 19% of the total body burden at the end of 24 hr of feeding on the tagged watercress leaves. Comparison of this value with 17% determined at equilibrium in the uptake experiments indicated that an equilibrium between body-water and tissue-bound compartments was established extremely rapidly. A concentration factor of 0.28 was determined for the ratio of whole-body tritium concentration in crickets to the tritium concentration in fresh plant material. This value was 30% of the concentration factor determined under equilibrium conditions. Utilizing data from both the uptake and elimination phases of this study, the ingestion rate

$$I = \frac{Q_i}{(p_1/\lambda_1) + (p_2/\lambda_2)} \quad (7)$$

Fig. 1.14. Patterns of tritium elimination in *Acheta* for body-water, tissue-bound, and whole-body components following a 24-hr feeding on tritium-tagged watercress.

in dpm ^3H /mg animal per day was determined to be 11.7. At equilibrium, an average cricket (400 mg fresh weight) would contain 19,880 dpm (8950 pCi) of tritium and would be ingesting and excreting 4680 dpm (2100 pCi) of tritium per day. Based on the assumptions that at equilibrium the tritium body burden is evenly distributed and that all beta particles given off from the whole-body tritium concentration are absorbed in the animal tissues, the dose rate to these animals would be 6.3 mrad/day. This resulted from a concentration of 0.5 $\mu\text{Ci}/\text{ml}$ in the water used to grow

the watercress - a value of five times the MPC for tritium in drinking water.

Annual consumption of ^{137}Cs - and ^{60}Co -labeled pine seeds by small mammals in an oak-hickory forest. Consumption rates of white pine (*Pinus strobus* L.) seeds by white-footed mice (*Peromyscus leucopus*) and short-tailed shrews (*Blarina brevicauda*) were determined in the laboratory and field. Following chronic feeding of ^{137}Cs - and ^{60}Co -tagged seeds, consumption rate was predicted from the equilibrium body burdens of ^{137}Cs . Laboratory variables affecting equilibrium levels were the feeding rate and, to a lesser extent, sex and temperature. As ingestion rates were increased (2, 10, 50, and 100 seeds per day), equilibrium body burdens of ^{137}Cs and ^{60}Co also increased proportionally (Fig. 1.15). Similarly, as temperature was increased between 4.4 and 21.1°C, the equilibrium body burden at each ingestion rate was also increased. For any temperature-ingestion rate combination, females acquired higher equilibrium than males.

This equilibrium technique was then applied to a mammal population in a mature second-growth oak-hickory forest of eastern Tennessee during July 1969 to September 1970. Field application of this technique was successful only because a dual-isotope tag was employed, using one isotope (^{137}Cs) which accumulated in tissues, and the second (^{60}Co) as a food tag with low assimilation. The ratio between the two isotopes during excretion in the laboratory was used to determine day of excretion for the field animals (Fig. 1.16). Based upon identical excretion rates of ^{137}Cs in both the laboratory and field, a direct correlation of seed consumption from laboratory to field was indicated (Fig. 1.17). The derived day of excretion, determined from the ratio between the two radioisotopes, was incorporated in the excretion equation from the laboratory to estimate equilibrium of ^{137}Cs for mice in the field. The equilibrium level was then corrected for the influences of sex and temperature and solved for the seed ingestion rate. Seed ingestion rates varied seasonally with a maximum consumption rate in summer of 2.3 g/mouse/day, and a minimum of 0.4 g/day in winter. Average yearly consumption rate was 1.6 g/day or 7.0 kcal/day. This was estimated to be approximately 45 to 50% of the total food consumption for this species.

The magnitude of seed consumption by the short-tailed shrew has been underestimated. Numerous studies have indicated that the shrew does consume seeds, but more interest has been shown in this as a curiosity of the species rather than in light of the destructive effect of such consumption. Seasonal seed

Fig. 1.15. Mean accumulation of ^{137}Cs in white-footed mice at 16 treatment combinations of temperature and chronic ingestion of white pine seed. Winter = 4.4°C ; autumn = 10.0°C ; spring = 15.6°C ; and summer = 21.1°C .

Fig. 1.16. Mean $^{137}\text{Cs}/^{60}\text{Co}$ ratios in white-footed mice during and following chronic ingestion of white pine seeds.

turnover rates of ingested radiocesium in the dominant earthworm species, and (3) estimating ^{137}Cs dispersion in the forest soil with laboratory soil-core microcosm studies utilizing ^{137}Cs -tagged leaf litter and *Lumbricus* earthworms.

The earthworm fauna of the forest was sampled six times during the year and was found to be composed of the endemic species *Octolasion icteum* and *Diplocardia udei*, with over 90% of the biomass contributed by *Octolasion*. *Octolasion lactum* is a deeply burrowing species which ingests mineral soil and incorporated organic detritus and rarely ventures into the upper litter layers. Extractable earthworm biomass was highest during the spring and autumn months, when soil moisture conditions are optimal (Table 1.13). Low biomass during the summer months is due in part to deep burrowing to avoid moisture stress and the appearance of young individuals in the population, as evidenced by the low modal weights. Radionuclide concentrations in earthworms, and hence their body burdens on a unit area basis, were highest in autumn immediately following input of new litter high in ^{137}Cs . Body burdens dropped precipitously during winter when feeding ceased, rose briefly in the spring, and then progressively declined throughout the remainder of the year as the organic litter supply was exhausted.

Turnover of ingested ^{134}Cs from leaf litter and from soil was determined for the earthworm *Octolasion* in laboratory studies. Parameters of biological retention were estimated by measuring the loss of an acute dose of ^{134}Cs through time. The estimated turnover rate for ^{134}Cs ingested as leaf litter was 0.036 hr^{-1} (biological half-life = 19 hr). For ingested ^{134}Cs -tagged soil, a turnover rate of 0.153 hr^{-1} (biological half-life = 4.5 hr) was obtained. The rapid rate obtained for soil-

cesium indicated that very little, if any, ingested radiocesium was assimilated from the soil, while the longer biological half-life for leaf-litter cesium (reduced turnover rate) indicated that some ingested radiocesium was assimilated into earthworm body tissues. The inability of *Octolasion* to assimilate appreciable amounts of radiocesium from tagged soil is consistent with previous reports that cesium becomes tightly bound to clay minerals. The results of experiments with tagged soil permit a calculation of soil turnover by *Octolasion*. Earthworms attained an equilibrium gut content (Q) of approximately 2 nCi of ^{137}Cs per earthworm. At this level, intake of radiocesium (I) is balanced by loss ($\lambda \cdot Q$), where λ is the loss rate coefficient. Therefore, $I = \lambda Q = (0.153 \text{ hr}^{-1}) (2 \text{ nCi}) = 0.3 \text{ nCi hr}^{-1}$. Dividing intake of radiocesium by the radiocesium concentration in soil (75 nCi g^{-1}) yields soil intake: 4 mg/hr. This was equivalent to a daily turnover of soil equivalent to 28% of the live body weight of the earthworm.

The role of earthworms in the vertical distribution of ^{137}Cs was evaluated in soil core microcosms using *Lumbricus terrestris*. An O_1 leaf litter layer, which consisted of ^{137}Cs -tagged *Liriodendron* leaves and upon which the earthworms fed, was placed on the microcosm soil surface. The results of radiocesium incorporation into the soil are shown in Fig. 1.18. The lined bars represent mean radiocesium concentrations for the three replicates, with standard errors of the mean shown by the stippled rectangles. Cesium-137 concentrations in the soil from earthworm feces increased with increased depth down to 30 cm. The radiocesium concentration then diminished rapidly and remained essentially constant to the bottom of the column. These results illustrate the ability of earthworms to redistribute radioactivity in the forest soil.

Table 1.13. Seasonal distribution of earthworm density, biomass, and radiocesium body burdens in the ^{137}Cs -tagged *Liriodendron tulipifera* forest

Values are means $\pm$ one standard error

Month	Modal wt (mg)	No./m ²	g dry wt/m ²	pCi/g dry wt ^a (N)	nCi/m ²
January	163	59.2	9.87 $\pm$ 1.32	26.6 $\pm$ 1.6(22)	0.26
April	94.7	133 $\pm$ 21.4	18.2 $\pm$ 0.65	317 $\pm$ 14(198)	5.76
May	119	70.5 $\pm$ 17.0	10.2 $\pm$ 0.46	147 $\pm$ 12(131)	1.50
June	21.5	25.0 $\pm$ 5.4	1.63 $\pm$ 0.16	236 $\pm$ 3.8(46)	0.38
August	85.1	108 $\pm$ 35.0	10.3 $\pm$ 0.18	153 $\pm$ 17(80)	1.58
September	130	133 $\pm$ 13.4	12.8 $\pm$ 0.66	418 $\pm$ 6(99)	5.35

^aExclusive of gut contents.

Fig. 1.18. Distribution of ^{137}Cs from tagged leaf litter in soil columns after 30 days of feeding by the earthworm *Lumbricus terrestris*.

MICROCOSMS: MANIPULATED EXPERIMENTAL SYSTEMS

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Microcosm techniques combined with multiple nuclide tracers and computer simulation of the system's dynamics provide an ideal tool for studying mechanisms and rates of mineral flow in the environment. Microcosm research is ideally suited for radionuclides where large-scale experimentation is not feasible, as well as to formulate specific research designs for field tests of ecological principles. Results of microcosm studies in terms of both small size and reduced complexity have preceded other small plot investigations or small-scale field studies. On the other hand, decreasing microcosm size and in particular complexity are analogous to investigations of microbiological, biological, and agricultural phenomena which usually involve one or two interacting components and a single environmental variable.

Microcosm research has demonstrated trends in radionuclide behavior in the environment which often are overlooked in the field because of system complexity and the simultaneous interactions of several environmental variables. Detection and quantification of trends of mineral movement in natural systems require large data inputs to eliminate natural but statistically important interferences. Precise replication in microcosms and control of system composition and environment

greatly reduces experimental variability. Thus microcosms form a bridge between field and classical laboratory experiments and provide an effective means for early detection of trends and measurement of fluxes of toxic and nutrient elements in the environment.

Cadmium Sorption-Removal by Soils and Sediments

Poisonous metals enter the environment primarily from liquid waste products of industry and secondly in rainout from air pollution. Their entrance into the food chain is mainly through small organisms which often constitute the food base for parts of man's diet. The relatively large surface-to-volume ratios of microbes and algae enable rapid contact uptake by the cells. Microcosm experiments were designed to measure uptake and removal of Cd in clay (illite), sand (quartz), and organic (leaf litter) sediment. Retention of atmospheric Cd was simulated by dripping "rain" twice a week at the average rate of precipitation in Oak Ridge (2.5 cm/week) on 2.5-cm-deep layers of litter and soil substrate. Average retention after three weeks of simulated rain was 98.5% of the added Cd in litter and 99.5% in soil. Thus organic and inorganic soil sorbed and accumulated Cd quantitatively from rainout.

Removal of Cd from litter and soil by Cd-free rain was measured in a subsequent microcosm experiment. During a three-week period less than 5% of the Cd was removed from litter, and less than 2.5% of the Cd in soil was leached by rainwater. Cadmium removal at each rainfall event was only 0.2 and 0.01% of the Cd content in litter and soil, respectively. These data confirm the tenacity with which Cd is retained by litter and in particular by inorganic soil (silt-loam), and the resulting inability of this element to be leached from litter and soil components of the system.

The role of biological retention of Cd in the soil profile as opposed to nonbiological adsorption by soil colloids was assessed by comparing Cd movement in soil which was sterilized with ethylene oxide gas as compared with soils containing natural microflora. The effect of the microflora on retention and subsequently on distribution of Cd in the profile is indicated in Fig. 1.19. Both sterile and nonsterile soil retained more than 99% of the Cd from the rainout. In nonsterile soil, however, 88% of the retained Cd was found in the top 6 mm of the profile, whereas this layer contained only 56% of the Cd retained in the sterile soil. Apparently soil microbiota, which normally are most numerous at the surface, assimilated and immobilized 32% of the added Cd, thus preventing subsequent transport to deeper horizons. This experiment underlines the impor-

tance of soil biota in the immobilization of Cd in surface layers and the subsequent effect of these organisms on Cd redistribution in the profile.

The same trends that were indicated for Cd sorption and immobilization from rainout by terrestrial substrates were found for Cd transfers to sediments in an aquatic environment. Aquatic microcosms consisted of aerated jars with about 10 cm of water over 2.5 cm of organic or inorganic sediment in which microbiota were added or excluded. More than 90% of the Cd which had been added to the water had been sorbed by the sediments within four days. Within one week an equilibrium was reached with only 1 to 3% of the Cd remaining in water for both inorganic and organic sediment systems. These results illustrate that, even in a static aquatic environment in contrast with the flowing conditions in the rainout and leaching experiments, there was a rapid and almost complete sorption of Cd by sediments.

Surface microbiota, as was the case in the terrestrial microcosms, influenced the vertical distribution of Cd in the sediment. Microbiota in the organic sediment contained 6% of the Cd in the system, and those in inorganic sediment had 3%. These differences are probably related to the greater growth of microbes on organic than on mainly inorganic sediment. Again, biota in the surface horizon immobilized much (20%) of the Cd in the profile and prevented subsequent diffusion to deeper layers (Fig. 1.19). Microbial immobilization was somewhat less in aquatic than in the terrestrial environment, presumably as a result of reduced microbial activity under the partially anaerobic conditions in submerged sediments, in contrast to the aerobic conditions at the surface of the terrestrial substrate.

These microcosm experiments clearly show that in a terrestrial system litter substrate initially retained less Cd than the mainly inorganic silt loam substrate, and that sorption of Cd from rain by terrestrial substrate is greater than uptake from water by similar aquatic sediment. The effect of microbiota on total retention of Cd by terrestrial substrate was apparent in its vertical distribution in the soil profile where microbial tissue immobilized Cd in the surface layer, reducing subsequent movement to deeper layers. In aquatic sediment, this effect was less pronounced, presumably as a result of less microbial activity on aerated soil than in anaerobic sediments.

Uptake of Cd and Zn by Snails

The animal component of Zn and Cd microcosms consisted of five small snails (*Contobasis clavaeformis*).

There was a rapid equilibration between snails and water because the standing crop of snails did not appreciably increase during the experiment. Maximum concentration in snail populations was reached within two weeks when snails contained about 35% of the Cd added to the system. The half-time for Cd elimination from snails to water was about one week, which indicated a rather rapid Cd turnover. When both algae and snails were added to the system about 8% more Cd disappeared from the water than with snails only. The initial rate of disappearance, however, was intermediate between those for algae and snails separately. Sediment, algae, and snails combined would remove 89% of the Cd and 98% of the Zn initially added to the water. Uptake of Zn by snails was slower than that of Cd, and the equilibrium of Zn between water and snails had not yet been attained within six weeks after addition of the isotope. Thus combined uptake of algae and snails was less than the sum of their separate uptakes. This was partly a result of reduction of the algal standing crop by snail grazing. Such examples of microcosm experiments using variations in system complexity, multiple isotope tagging, and analog computer simulation of system dynamics and isotope flow demonstrate the merit of this technique in initial assessments of the fate and dangers of toxic substances released into the environment. Small-scale studies provide insight and understanding on mechanisms, pathways, and transfer rates involving toxic metals in the environment. Such data are valuable prerequisites to field-scale investigations and further implementation of remedial action for improving environmental quality.

Fig. 1.19. Vertical distribution of Cd by (A) silt loam soil in terrestrial microcosms and by (B) sorption on silt loam sediment in aquatic microcosms. Cadmium was applied to (A) as rainout and leached by successive rainfall events. Both microcosms were incubated for three weeks.

Uptake and Release of Cd, Zn, and Hg by Bacteria and Algae

Microcosm techniques were used to evaluate the role of microbiota in transfers of toxic metals. Multiple-isotope tags were applied to the water compartment of aquatic microcosms which contained several combinations of biota, viz., mixed natural populations of bacteria, algae. A special technique involving injection of the algal suspension into solutions had to be used in order to follow the rapid initial uptake of metals by the biota. Cultures were maintained over Millipore filters so that the biotic component could be extracted and measured during short time intervals after introductions of Cd and Zn. Maximum concentrations of Hg and Zn mixed in algal populations were attained within 15 sec. Uptake time for Cd was slightly longer; between 15 sec and 5 min transpired before equilibrium between Cd in water and algae was attained.

At equilibrium concentration, algal tissue contained roughly 1000 times more Cd, 250 times more Hg, and 1250 times more Zn than an equivalent quantity of water. Roughly half of the uptake appeared to be nonbiological adsorption, and this was completed within 5 sec. External sorption was indicated as the initial mode of uptake because metal concentration of freshly killed cells was approximately half that of living cells. Compared with living algae, after 5 sec the dead cells contained 40, 75, and 50% of the equilibrium concentrations of Cd, Hg, and Zn, respectively. Thus there was a significant instantaneous adsorption of toxic metals into algal cells followed by a slightly slower uptake into the living cells which approximately doubled the total amount of adsorbed metal. After the rapid initial uptake of metals from water, the microbiota continued to accumulate metals, and this was attributed to additional biotic growth in the microcosm. Some of the uptake was an "aufwuchs" on the walls of the containers. These organisms eventually formed an effective barrier against metal diffusion into the plastic walls, analogous to effects caused by microbiota on sediment surfaces.

In nonsterile systems, bacteria in a sand sediment decreased Cd concentration in water to less than half that in sterile sediment (Fig. 1.20). Equilibrium concentrations in sediment and water had not yet occurred after five weeks, primarily because gross movement of Cd from sediment (including bacteria) to water was less than from sterile sediment to water. Analog simulations of these transfers indicated half-times ($t/2$) for gross movement of 35 days and less than 3 days for nonsterile and sterile sediments, respectively. Algal

Fig. 1.20. Disappearance of Cd from the water compartment of microcosms which contain sediment, and with or without bacteria, algae, and snails, during six weeks of incubation.

populations in microcosms assimilated slightly less Cd than the bacteria, and gross transfer of Cd from algae to water was even slower than when bacteria were present. Half-time loss for Cd in this pathway was more than two months.

Slow release of biologically immobilized minerals from bacterial and algal populations measured in weeks and months is in sharp contrast with the rapid uptake measured in seconds and minutes. Two apparent reasons for the slow release are recycling of assimilated or adsorbed minerals from senescent and dying organisms to young and growing ones within the population, and the increase in standing crop of these organisms, in particular in the form of "aufwuchs," during the experiment.

Thus uptake of Cd and other tested toxic metals by microbiota in the aquatic environment is initially very rapid and partly nonbiological. The rapid initial uptake phase is followed by continued uptake by the growing population and increasing standing crop. This increasing accumulation of metals by the growing population may be found in a parallel accumulation in a static population downstream from an outfall source of metals.

^{137}Cs Transfer to Primary Producers

In contrast to toxic metals which mainly enter the aquatic food chain through microbiotic pathways, entry

Table 1.14. Distribution of weight and ^{137}Cs in litter, soil organic matter, and tree seedlings in microcosms incubated for five months and leached by simulated rain (2.5 cm/week)

Values are means of triplicate systems

	Weight (g)			^{137}Cs content (% of total)		
	Litter	Soil organic matter	Seedlings (x 1000)	Litter	Soil organic matter	Seedlings
No fauna	4.73	0.10	0.16	86.1	1.9	0.7
Millipedes	3.63	0.66	0.22	46.4	17.7	2.8
Snails	4.08	0.23	0.14	67.9	5.7	1.1
Both species	2.75	0.77	0.20	35.4	21.0	2.5

of nutrient elements into foodstuffs primarily involves terrestrial macrophytes. Much of the nutrient capital is recycled from detritus of primary production back to plants. Significant effects by microflora, snails, and millipedes on the release of ^{137}Cs from tree litter were reported earlier,⁴⁰ and additional studies have focused on the effect of faunal fragmentation of litter, on release of a nutrient analog ^{137}Cs , and on subsequent uptake of the tracer by tree seedlings. The effects of snails and millipedes on uptake of ^{137}Cs by seedlings was significant ($P < 5\%$). Both species increased the ^{137}Cs content of seedlings, but the effect was less for snails than for millipedes (Table 1.14). Snails fed directly on the plants and reduced the standing crop; snails deposited excrements mainly on top of the litter whereas millipedes incorporated three times more organic detritus into the sand than did the snails. Greater mineral availability from excrements which were dispersed throughout the rooting medium (millipede effect) as opposed to excrement concentrations in litter (snail effect) resulted in more ^{137}Cs uptake by plants as a result of millipede mixing of materials. When both animal species were combined, values of intermediate standing crop and ^{137}Cs content were between those of systems which contained only one species. This microcosm study demonstrates significant direct and indirect effects of soil fauna on growth and mineral uptake by tree seedlings. Thus the importance of soil fauna is not limited to litter decomposition, and their effect on primary production should be included in models of ecosystem production and mineral flow.

40. M. Witkamp and M. L. Frank, pp. 635-43 in *Cesium-137 Kinetics in Terrestrial Microcosms*, Proc. 2nd Natl. Symp. Radiocology, Ann Arbor, Mich., D. J. Nelson and F. C. Evans (eds.), CONF-670503, TID-4500, 1969.

ECOSYSTEM ANALYSIS

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The dynamic aspects of ecological processes are emphasized in modeling the flux of materials in ecosystems. Experimentally derived flux rate parameters are used with systems analysis techniques to develop ecosystem models which are important tools for predicting the fate of radioactivity in the environment. This approach has been applied to the determination of cycling rates of ^{137}Cs in a *Liriodendron tulipifera* L. forest ecosystem.

Model of ^{137}Cs Behavior in Plant and Soil Components of a Forest Ecosystem

Nearly ten years ago, a *Liriodendron* forest was tagged with ^{137}Cs to elucidate pathways and rates of radioactivity movement among the major components.⁴¹ Between forest tagging in 1962 and resurveys through 1970, most *Liriodendron* trees showed a 100-fold decrease in ^{137}Cs of late spring foliage. Diminished concentration in foliage suggested redistribution within trees and soil. Generalized income-loss models, which initially utilized constant coefficient transfer parameters, characterized ecosystem behavior in very general terms.⁴² These constant coefficient models which described first-season redistribution of ^{137}Cs indicated that abrupt transient changes resulted from shifts and even reversal of a dynamic balance of income and loss rates. For short periods, the coeffi-

41. J. S. Olson et al., *Health Phys. Div. Annu. Progr. Rep. July 31, 1963*, ORNL-3492, pp. 100-106.

42. J. S. Olson, *Health Phys.* 11(12), 1385-92 (1965).

cient of transfer could be characterized by average values, but even these would change from summer through autumn and winter. Data from successive years suggested that each year had a cycle in which certain exchange coefficients could be expressed as a function of the day of year, without relating seasonal changes to the physiological controls which brought them about.

General trends shown by Fig. 1.21 support the prediction made early in the project: that cesium is very mobile within the living part of the ecosystem, and the nuclide becomes immobilized as it passes into the inorganic medium.⁴³ In Fig. 1.21A, the inoculum of ^{137}Cs into stem decreased rapidly in wood, and this suggests important redistribution via phloem transport tissue. During each vernal period, there was a rapid upward movement of the isotope, along with the usual flush of nutrients into the new crop of leaves (B). The leaf component lost radioactivity during the summer from leaching and redistribution of cesium (and presumably other alkali metals), and finally leaves returned to the forest floor as litterfall. Meanwhile, further downward translocation to the phloem carried a significant reserve of these materials to the roots (C). This reserve was depleted each spring by upward translocation to the new flush of leaf growth.

Transfer to the litter layer of the forest began well before the main fall of leaves to the forest floor, not only because of rain leaching but because of feeding by canopy insects and movement of these, or their frass, or their predators to the ground. Leaf fall contributed a distinct Autumn "spike" to the litter layer in the early years, but later as the concentration in leaves decreased there was a more nearly continuous balance of income and loss. In fact, fluctuations were even less marked than shown in Fig. 1.21D because of gradual admixture of inorganic material upward into the litter layer which resulted from activities of soil and fauna. Radiocesium increases in soil (Fig. 1.21E) were attributed to the root-to-soil transfer pathway because roots were dispersed extensively through the soil. The rapid buildup of ^{137}Cs in the mineral parts of the soil resulted from root contribution, and this pathway contributed even more radiocesium to soil than from the downward infiltration of this nuclide from the litter layer.

Several changes in the model of Cs dynamics in a forested system were suggested by this simulation. The wood compartment ideally should be partitioned to separate sapwood, where there was rapid movement of salts, from inner wood (probably heartwood) where a reservoir of relatively immobile cesium remained in the trees until the nuclide was released by mortality and

Fig. 1.21. Dynamic redistribution of ^{137}Cs in major components of the tagged *Liriodendron* forest. Solid lines are simulations and dotted lines represent observed values. Radiocesium was injected into tree bole on May 22, 1962.

decomposition. The mineral soil not only contained an increasing fraction of the total radiocesium on the plot, but also possessed components which were even less likely to be remobilized than the soil fractions which initially received radiocesium from roots and litter.

Simulations in Fig. 1.21 do not yet represent the best adjustment of model parameters with empirical data from remeasurement, but they approximate the main seasonal variations of radiocesium in the forest ecosystem. Certain components are still pooled as subsystems in the present model, although more detailed modeling of litter subsystems has been made in the past year.⁴⁴ These improvements are important for interpreting radiocesium cycling in forested ecosystems. Further refinement in process models will strengthen our ability to predict the fate of radioactivity in terrestrial landscapes.

43. J. S. Olson, *Health Phys. Div. Annu. Progr. Rep. July 31, 1966*, ORNL-4007, p. 119.

44. J. S. Olson, in *Third National Symposium on Radiocology*, AEC-CONF-710501 (in press).

2. Walker Branch Watershed: A Study of Terrestrial and Aquatic System Interaction

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In the past half century technology aimed at achieving a higher standard of living has progressed more rapidly than an understanding of the deleterious effects of this technology on the environment. In forestry, timber demands diminished old-growth forest reserves to the point where foresters began developing techniques for improving production and utilization of second-growth forests and plantations. Many of these techniques, that is, clearcutting and fertilization, have recently been attacked as being detrimental to the landscape and water quality.

General objectives of the Walker Branch watershed project on land-water interaction are twofold: (1) to quantify the relationships between terrestrial and aquatic productivity, mineral balance, and water quality in a natural forested ecosystem and (2) to assess quantitatively the impact of a relatively new silvicultural technique, forest fertilization, on these relationships. Emphasis of this project is on elucidating the structure and functioning of both terrestrial and aquatic systems and interactions between them. The end product of this research will improve our understanding of forested systems and hopefully contribute to formulation of a rationale to be employed in evaluating land management techniques.

Last year's annual report⁴ outlined the following specific objectives of the Walker Branch project:

1. relate water quality and stream productivity to characteristics of the adjacent terrestrial system, especially with regard to mineral cycling.
2. establish the relationship between the hydrologic and mineral cycles.
3. provide "baseline" information on natural terrestrial-aquatic ecosystem interactions for comparison with those modified by cultural treatments.
4. apply the knowledge gained from this small, controlled drainage basin study to broader landscape units to evaluate the impact of man's activities on the total ecosystem.

These objectives are consistent with those of the International Biological Program (IBP) effort now underway in the Ecological Sciences Division (see IBP section in this report); IBP research is being conducted at three levels of research identified as physiological processes, stand, and watershed units. Walker Branch watershed is the site on which watershed level research is being conducted, and as such the scope of the watershed project has broadened during the past year.

Mineral budgets, water yields, and terrestrial and aquatic productivity of the watershed will be used to test the applicability of models developed from more detailed research on process mechanisms of forest stands. Manipulation of the watershed by fertilization will provide an experimental nutrient pulse to an undisturbed system enabling us to validate models describing growth dynamics, litter decomposition, and nutrient movement. At the same time, continuing studies on the watershed will allow us to identify

1. Dual capacity.

2. NSF summer research participant.

3. U.S. Geological Survey.

4. S. I. Auerbach et al., *Ecological Sciences Div. Annu. Progr. Rep.* July 31, 1970, ORNL-4634, pp. 82-102.

important ecosystem parameters which are responsive to manipulation. Such identification will enable us to concentrate research efforts on these parameters.

This progress report presents results of studies designed to characterize components of the undisturbed system including:

1. further characterization of hydrologic and mineral input to and output from Walker Branch,
2. characterization of the geology and past land-use history of the watershed,
3. data on growth dynamics ascertained from a re-measurement of the permanent growth plots three years after their initial measurement,
4. temporal changes in nutrient contents of foliage and associated litterfall for major tree species found on the watershed,
5. preliminary findings on nutrient pools in the litter-soil system,
6. additional information on aquatic productivity,
7. features of a simulation model for predicting evapotranspiration and soil moisture changes in response to meteorological inputs.

TERRESTRIAL STUDIES

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Vegetation Analysis and Forest Stand Production

During the past year the 298 permanent plots established in 1967 were resurveyed. Diameter, ingrowth, and mortality of new and previously tallied trees were measured. Tree mortality was partitioned into standing dead and fallen individuals. Table 2.1 summarizes average stand basal area contributed by the 12 major species with 95% of total basal area for the four forest types recognized on the watershed. Major changes were in the chestnut oak and pine forest types. Chestnut oak stands are relatively younger with higher density resulting in greater overall net basal area growth. The negative change in basal area of pine stands reflects mortality of larger trees due to natural successional change in overmature stands and the effects of a wildfire which occurred in the spring of 1967. The effects of fire and overmaturity appear to be confounded. A more extensive analysis of seedling dynamics is to be initiated, since this component undergoes annual changes not discernible in the present survey procedure.

Table 2.1. Total basal area (m^2/ha) of 12 major species in major forest types of Walker Branch watershed^a

Forest type	1967	1970	Net change
Oak hickory	20.08	20.04	0.76
Chestnut oak	24.85	25.81	1.76
Mesophytic hardwood	21.18	21.83	0.65
Pine	23.91	23.04	0.87

^aMortality and ingrowth are incorporated in calculation of basal area.

With the completion of a second plot survey and development of general allometric functions of LPP primary production section, a stand biomass and turnover budget was completed. The allometric proportion of stand biomass and mortality was supplemented by additional harvests of major species on Walker Branch watershed to verify general allometric functions and determine baseline mineral nutrient levels. Table 2.2 summarizes aboveground biomass, net production, and mortality for the dominant oak-hickory forest type. Net production amounts to 7622 kg/ha of which 56% is leaf production that is contributed annually to the litter. Annual mortality amounts to 956 kg/ha or 1% of the total standing biomass prior to leaf fall. Most of the biomass lost through mortality remains as standing dead material (Table 2.3) and is subject to some degree of decay and leaching of mineral nutrients. Only 12% of the annual mortality can be expected to be transferred to the litter that same year. Experiments are in progress to evaluate the significance of residence time of standing dead material. The persistence of standing dead material may be a natural feedback controlling the release of mineral nutrients. Forest cutting operations, which result in slash accumulation, increase the amount of substrate subject to decay and mineralization, thus resulting in mineral inputs to soil in excess of stand requirements. Complete forest product utilization (reducing slash accumulation) with controlled fertilizer application may result in lessened impact on water quality during forest management.

Past forest growth is being reconstructed for increment core data collected from 900 individual trees over the range of site conditions present on Walker Branch watershed. This information will be used to develop a productivity profile for the basin which simulates past forest growth rates and projects future response for different site conditions. Other work in progress is the development of allometric functions to estimate stand root biomass (of LPP primary production

Table 2.2. Summary of aboveground biomass, net production, and mortality for oak-hickory forest type on Walker Branch watershed

Forest type	Standing biomass 1970 (kg/ha)	Net production per year (kg/ha) ^a			Biomass lost through mortality per year
		Stem	Branch	Leaf	
Oak-hickory	117,918	2654	695	4273	956

^aCalculated from difference between 1967-1970 standing biomass less mortality, but including ingrowth.

Table 2.3. Summary of transfer of bole and branch biomass to litter layer of oak-hickory forest type on Walker Branch watershed

Forest type	Total loss through mortality per year (kg/ha)	Standing dead biomass per year (kg/ha)	Input to litter layer per year (kg/ha)
Oak-hickory	956	840	116

section). A better understanding of this component is essential to baseline characterization prior to planned fertilizer application.

Nutrient Concentrations Associated with Foliage

Nutrient concentrations associated with temporal leaf development were studied for ten tree species which are major basal area contributors on Walker Branch watershed. At each sampling date, 25 leaves were collected from each tree, dried to constant weight, and analyzed for N, P, K, and Ca. Weights and nutrient concentrations are reported as means of observations for each tree species. Standard errors are generally less than 10% of their associated means.

Seasonal dry weight changes for leaf units of each species and differences in date of leaf drop for the various species are shown in Fig. 2.1. Leaf units are individual leaves for all species except hickory, where an individual leaflet is considered a leaf unit, and pine, where a fascicle is regarded as a leaf unit. Leaves of all hardwood species increase rapidly in weight during May and then either level off (hickory, sourwood, black gum, and red maple) or continue to grow at a decreased rate (oaks and tulip poplar) until a month or six weeks prior to leaf fall when some weight reduction is evidenced. Pine species maintain relatively constant weights throughout the year; however, newly initiated needles were not included in these samples. Tulip poplar, black gum, and sourwood fall earliest (mid-October), followed by red maple, hickory, chestnut oak, and northern red oak (late October to early

November), while white oak holds its leaves until mid to late November.

Figures 2.2 and 2.3 present seasonal leaf concentrations of N and P, respectively. Nitrogen and phosphorus concentrations of deciduous species generally decrease as leaf development progresses, whereas concentrations in pine remain relatively constant. Concentration differences among deciduous species are small, although some show early season differences. Additional data analysis is being undertaken to determine to what extent decreases in N and P concentrations are the result of greater leaf biomass. This analysis should also yield seasonal differences in uptake rates.

Potassium concentrations (Fig. 2.4) are much more variable than those for other elements. After initial decreases similar to N and P, K concentrations in leaves behave differently for the various species. Concentrations in tulip poplar, red oak, chestnut oak, and red maple continue to decrease through the growing season; concentrations in the other four deciduous species fluctuate with no apparent pattern. The increase in K concentration in sourwood foliage right up to the time of leaf drop is interesting in view of the general conception that potassium in leaves is highly susceptible to leaching losses just preceding leaf fall. Levels of potassium in pine remain fairly constant throughout the season.

Calcium concentrations increase in deciduous foliage throughout the growing season (Fig. 2.5). This increase parallels leaf growth (weight) and is consistent with the

Fig. 2.1. Seasonal foliage dry weight of eight deciduous and two pine species on Walker Branch watershed. Leaf units are individual leaves for all species except hickory and pine where leaflets and fascicles, respectively, are regarded as a leaf unit.

Fig. 2.2. Seasonal nitrogen concentrations (percent of dry weight) in leaves of eight deciduous and two pine species on Walker Branch watershed.

Fig. 2.3. Seasonal phosphorus concentrations (percent dry weight) in leaves of eight deciduous and two pine species on Walker Branch watershed.

Fig. 2.4. Seasonal potassium concentrations (percent dry weight) in leaves of eight deciduous and two pine species on Walker Branch watershed.

Fig. 2.5. Seasonal calcium concentrations (percent dry weight) in leaves of eight deciduous and two pine species on Walker Branch watershed.

role of Ca as a structural constituent of cell walls. In contrast to N and P, Ca is not diluted by growth and must be supplied to the foliage throughout the season as opposed to an initial intake followed by translocation within the foliage. The higher concentrations apparent in tulip poplar and hickory reflect inherent variation among deciduous trees in Ca accumulation and pose questions concerning differential physiological demands for calcium by various tree species

Nutrient Content of Litterfall

Nutrient input to the forest floor via leaf fall, a major transfer mechanism from vegetation to soil, was investigated on the watershed using 80 1-m² litter traps. The temporal patterns of litterfall were shown in last year's annual report.⁴ This past year nitrogen, phosphorus, potassium, and calcium analyses were completed on this litterfall material, and results of those determinations follow.

Figures 2.6 to 2.10 present total amounts of litter, N, P, K, and Ca, respectively, returned annually to the forest floor in four forest types on Walker Branch watershed. Leaves account for over 75% of the litterfall input in terms of weight and nutrients for all forest types. There is no significant difference in biomass input among the forest types and little difference in the amount of nutrients returned, although calcium and potassium return tends to be greater in mesophytic hardwood stands and potassium greater in oak-hickory.

Figures 2.11 to 2.14 show concentrations (percent dry weight) of N, P, K, and Ca in litterfall throughout the year. During the growing season, concentrations of all elements in litterfall are lowest during periods of leaf drop. Concentrations of N, P, K, and Ca differ little among the four forest types.

Litter Biomass and Nutrients

Mineral pools in soil organic and mineral horizons, decaying wood, and herbaceous vegetation are being examined to assess seasonal variations in their relative size with respect to the overstory vegetation types and slopes present on the watershed. Mineral transfers due to throughfall leaching and litterfall are also being measured. Since April 1971, three 1-m² subplots in each of 24 plots (six in each of four vegetation types covering a range of slopes from 5 to 55%) have been sampled at two-month intervals. Dry weight and concentrations of N, P, K, Ca, Mg, and Na are being determined for the components mentioned above. Dry weights of O₁ and O₂ horizons of the forest floor in the

Fig. 2.6. Annual dry weight of litterfall components (Grass, Stems, Other, Leaves) in four forest types on Walker Branch watershed. The component entitled "other" consists mainly of reproductive parts and bud scales.

Fig. 2.7. Annual nitrogen return in four forest types on Walker Branch watershed. The component entitled "other" consists mainly of reproductive parts and bud scales.

Fig. 2.8. Annual phosphorus return in four forest types on Walker Branch watershed. The component entitled "other" consists mainly of reproductive parts and bud scales.

Fig. 2.9. Annual potassium return in four forest types on Walker Branch watershed. The component entitled "Other" consists mainly of reproductive parts and bud scales.

Fig. 2.10. Annual calcium return in four forest types on Walker Branch watershed. The component entitled "other" consists mainly of reproductive parts and bud scales.

Fig. 2.11. Temporal concentration of nitrogen in the leaf component of litterfall for four forest types on Walker Branch watershed.

Fig. 2.12. Temporal concentration of phosphorus in the leaf component of litterfall for four forest types on Walker Branch watershed.

Fig. 2.13. Temporal concentration of potassium in the leaf component of litterfall for four forest types on Walker Branch watershed.

yellow poplar and oak-hickory vegetation types as affected by slope are shown in Fig. 2.15.

Organic matter accumulation is greater in the oak-hickory vegetation type than in the yellow poplar type for slope classes up to 35% but tends to equalize on

Fig. 2.14. Temporal concentration of calcium in the leaf component of litterfall for four forest types on Walker Branch watershed.

Fig. 2.15. Dry weight of organic horizons under yellow poplar and oak-hickory stands as influenced by slope on Walker Branch watershed.

greater slopes. This convergence is due in part to the greater occurrence of oak and hickory in yellow poplar stands on steeper slopes where they are transitional to the oak-hickory vegetation type, and partly to the effects of overland flow on steep slopes which is capable of transporting organic materials to lower slope positions and stream channels. Over twice as much organic matter accumulates on the forest floor of oak-hickory stands as does in those of yellow poplar. The relative contribution of the O₂ horizon to the total forest floor is greater in oak-hickory than yellow poplar stands. The forest floor acts as a moisture and nutrient reservoir for a stand, and the above data, together with preliminary nutrient concentrations, indicate that yellow poplar stands recycle nutrients faster than oak-hickory stands possibly resulting in greater growth, but also the smaller litter accumulation offers less buffering against nutrient losses due to leaching. Litter accumulation patterns in chestnut oak and pine vegetation types are similar to those shown for oak-hickory. Standard errors range from 10 to 25% of the mean for all vegetation types and are indicative of the variations found in hardwood stands.

Soil Moisture and Evapotranspiration Simulation Model⁵

A digital computer model, SOGGY, has been developed to simulate soil moisture changes in response to

5. Detailed report in pp. 795-800 of the *Summer Computer Simulation Conference*, July 19-21, 1971, Boston, Mass.

meteorological inputs. SOGGY will be used in models describing forest growth, hydrologic response, and nutrient movement on Walker Branch watershed. The model (Fig. 2.16) is based on the general hydrologic balance

$$P = ET + RO + S,$$

where P is precipitation, ET is evapotranspiration including water intercepted by vegetation, RO is runoff or water moving from the rooting zone to groundwater or streamflow, and S represents water stored in soil for periods longer than those under consideration.

SOGGY requires initial inputs of data concerning physical properties of the soil under consideration and utilizes simple assumptions regarding water storage and movement in soils. Daily meteorological inputs include solar radiation, dewpoint, temperature, wind speed, and precipitation. The general mechanics of SOGGY are shown in Fig. 2.17. Initial soil parameters are set for moisture content, moisture tension-moisture content relationships, and pore space of surface and subsurface horizons which are 10 and 150 cm thick, respectively. This horizon separation is based on depths and root densities observed for soils on the watershed. Meteorological data are read and potential evapotranspiration (PE) is computed using a combined energy-balance, aerodynamic approach⁶ which considers a seasonal factor and radiation from the watershed in addition to meteorological inputs mentioned previously. Potential evapotranspiration is apportioned on the basis of relative root densities in the surface and subsurface horizons which are assumed to be 0.2 and 0.8, respectively. Actual evapotranspiration (ET) for each horizon is then calculated based on tensions at which water is held by the soil and the magnitude of PE. Figure 2.18 characterizes this relationship. After water has been lost from each horizon, new moisture contents and tensions are printed, moisture tensions in the two horizons are equilibrated by allowing water to flow from one to the other, meteorological data for the next day are read, and the cycle repeated.

If rainfall occurs during a day the sequence changes depending on rainfall amount and antecedent soil moisture conditions. The first step is to diminish rainfall to account for vegetation interception which is evaporated daily regardless of potential evapotranspiration. During the growing season 1.4 mm of the total rainfall is allocated to interception, whereas this factor drops to 0.4 mm during winter. After interception losses have been satisfied the surface horizon is

Fig. 2.16. Components of the water balance considered in SOGGY, an evapotranspiration model.

wetted to field capacity, the subsurface horizon is treated likewise, and finally excess water accumulates within soil pores. If, following a rain, soil moisture is held at lower tension in the surface than in the subsurface horizon, water loss occurs exclusively from the surface until its tension again reaches that of the subsurface. Tensions are then equilibrated and the cycle continues as in the nonrain condition. If the entire soil profile is wetted above field capacity, excess water is lost by both evapotranspiration and drainage. Evapotranspiration proceeds at the potential rate, and water in excess of that is drained at an exponential rate so that field capacity is attained within three days.

SOGGY has yet to be evaluated completely but appears able to provide relative seasonal and annual soil moisture status data necessary to model hydrologic and biomass accretion phenomena. As shown in Table 2.4, SOGGY reasonably estimates the annual water balance of Walker Branch watershed for 1969. SOGGY has not yet been applied to other soil-climatic conditions, but there is reason to believe that the relationships used are of general applicability. Initial input of soil moisture-release curves and rooting depths and densities need to be representative of the area under consideration in order for SOGGY to perform a realistic simulation.

Land Use History

Prior to acquisition by the U.S. government in 1942, the AEC Oak Ridge Reservation was primarily in-

6. H. L. Penman. *Neth. J. Agr. Sci.* 4, 9 (1956).

Fig. 2.17. Generalized flow chart of SOGGY (evapotranspiration model) simulation.

habited by agriculturally oriented families. Land settlement progressed from the major river bottoms and terraces up the minor stream courses to the ridgetops. Thus, population densities and intensity of agriculture activity decreased from river bottoms to ridgetops, reflecting the suitability of the land for cultivation. Walker Branch watershed lies on the southern slope of Chestnut Ridge and was less intensively managed than adjacent land along the Clinch River. In spite of the steep slopes (average approximately 30%) and shallow soils, cultivation and other agricultural and forestry practices were practiced in the area and influenced subsequent vegetation and soil characteristics. The study reported here was designed to identify manage-

ment practices conducted on the watershed and delineate their aerial extent. The type of information collected included:

1. names of landowners and locations of their homes,
2. types of crops and livestock raised by the inhabitants,
3. agricultural techniques with long-term effects on vegetation and soil,
4. lumbering activities and policies,
5. history and extent of fire,
6. locations of forested, cultivated, and pastured fields in 1935-42.

Table 2.4. Annual water balance of Walker Branch watershed - 1969

	Measured (cm)	Estimate 1 ^a (cm)	Estimate 2 ^b (cm)	Estimate 3 ^c (cm)
Evaporation	73.6	72.9	65.5	75
Runoff	51.6	52.3	39.7	50
Precipitation	125.2	125.2	125.2	125

^aEstimated daily by SOGGY.

^bEstimated daily by combination energy-balance aerodynamic approach [O. T. Denmead and R. H. Shaw, *Agron. J.* 45, 385 (1967)].

^cEstimated monthly by Thornthwaite's method [C. W. Thornthwaite and J. R. Mather, *Climatology* 10(3) (1957)].

Fig. 2.18. Change in ratio of actual to potential evapotranspiration with change in soil moisture tension and in potential evapotranspiration (based on data of Denmead and Shaw) [O. T. Denmead and R. H. Shaw, *Agron. J.* 45, 385 (1967)]. This relationship was used to calculate actual evapotranspiration in SOGGY, an evapotranspiration model.

This information will aid in establishing relationships between present soil characteristics and their associated vegetation, especially with regard to mineral nutrition and water regimes.

Aerial photographs taken in 1924, 1935, 1938, 1952, 1956, 1959, and 1967 were used to establish land use boundaries and provided an initial assessment of cultural practices employed in the area. These photographs did not reveal all management practices, and an intensive effort was made to locate and interview the previous inhabitants of the area. Extensive field verification was used to substantiate both the recollections of these people and interpretations of aerial photos.

Eleven families owned land on the watershed prior to acquisition by the Corps of Engineers in 1942. There

were four homesites located directly on the 241-acre watershed, but two farmers owned 179 acres. Two main roads served the area; one ran along the western boundary of the watershed and connected the valleys on either side of Chestnut Ridge while the other followed Walker Branch, split at the confluence of the east and west fork, and extended up both stream bottoms before terminating at homesites. There were numerous farm and logging roads throughout the watershed, but these were used infrequently.

The land management of the area immediately prior to 1942 varied greatly depending upon the topography and fertility of the land and the needs of individual owners. Seven major land use areas are delineated in Fig. 2.19, and descriptions of the areas are given in Table 2.5. Agriculture was practiced on 21% of the watershed in varying degrees of intensity. Most farming was of the subsistence type, the notable exception being area 5A which yielded some vegetables and flowers for sale at local markets. The gardens provided food for family consumption, while fields yielded hay and corn for livestock feed with some corn undoubtedly diverted to whiskey manufacture. A technique commonly used in subsistence agriculture was practiced on the watershed, particularly in areas 4A and 4B. Land on steep slopes was cleared and subsequently cultivated until decreased fertility and erosion limited crop yields. These areas were allowed to revegetate and were then pastured, often with burning used to control brush and sage grass. Fields were burned in the winter and pastured the following spring and summer. Occasionally a field was allowed to lie fallow two or three years in order to increase soil organic matter content and then cultivated again for one or two years. Both of these practices caused severe erosion and soil degradation which eventually led to abandonment or conversion to woodland pasture. Land owners practiced little forest management prior to 1942. They cut small

WALKER BRANCH WATERSHED
LAND USE AREAS

Fig. 2.19. Land use areas on Walker Branch watershed superimposed on 1935 photograph of the area. Descriptions of land use areas are given in Table 2.5.

Table 2.5. Descriptions of land use areas delineated on Walker Branch watershed in Fig. 2.19

Area	
1	Homesite with small cabin in the bottom of west fork; rock walls and flower beds; lawn and garden maintained immediately north and west of cabin; no large-scale farming practiced due to narrowness of valley.
2	Two large fields on gently sloping ridgetop which extend beyond boundary of watershed; corn primarily raised without fertilizer addition; no severe erosion evidence.
3	Pasture on gently sloping ridgetop extending onto upper slopes which are somewhat steeper; some erosion on steeper slopes; area severely burned in 1967 causing complete seedling and sapling mortality as well as some in overstory.
4	This area represents the agriculture complex of the owner and is broken down into the following sections:
4A & 4B	Areas on steep lower and middle slopes alternately used for pasture and cultivated crops; burn and graze type of agriculture; advanced sheet and gully erosion active in 1942; mostly burned in 1967.
4C	Level bottom in east fork; homesite with outbuildings in northwest portion; extensive gardens and several fruit and walnut trees; some better pasture; road ran through this area.
4D	Pastured woodlot on steep to gentle slopes; probably better timber selectively removed; area subjected to burn from fire escaping from areas 4A and B.
5	Extensively cultivated area on gentle ridgetops grading to steeper upper position slopes; divided into following areas:
5A	Predominantly gently sloping ridgetop; large commercial vegetable garden and hay and corn fields; erosion evidence slight; barn occupied southwest portion of this area.
5B	Pasture on fairly steep slopes; heavily used prior to 1930 when partially abandoned due to severe erosion.
5C	Western portion of this area was a woodlot until 1930 when it was partially cleared for pasture. Eastern portion was a productive corn and hay field; fertilization and crop rotation were apparently practiced. Entire area was planted to loblolly pine in 1951 or 1952.
6	Predominantly a pastured area which changed repeatedly between 1924 and 1942; gently sloping ridgetop with small cabin; A is oldest cleared area while B is most recently cleared.
7	Bulk of watershed; steep topography with relatively undisturbed deciduous forest; oak trees selectively cut for railroad ties; certain areas may have been used more extensively for agriculture prior to 1900's.

quantities of timber for their own use in building construction, fence rails, and firewood. They also sold some timber to neighbors who selectively harvested larger oaks for use as railroad ties.

It is difficult to assess the total impact of fire on Walker Branch watershed. It is assumed that most of the area has burned periodically throughout its history. Fires probably escaped from pastures where fire was used to control brush. These fires were not severe and consumed only ground cover and some of the soil organic layer; however, they undoubtedly contributed to some soil degradation due to increased erosion and susceptibility of nutrients to leaching.

In 1967 two fires burned parts of the watershed shown in Fig. 2.20. One of these burned only four acres on the west watershed and had limited effect on the vegetational structure. The other was more severe, burning a total of 86 acres, mostly on the east watershed. This fire was extremely hot on the ridge-

tops, as evidenced by charred trunks as high as 4 m above-ground, but decreased in intensity as it burned downslope. Since 1967 vegetation patterns in the more severely burned areas have changed appreciably. Most of the understory and some overstory trees have died with a resultant upsurge in herbaceous and woody undergrowth. A comparison of adjacent burned and unburned acres is shown in Fig. 2.20. Both fires combined burned 38% of the total watershed area with about 15% burning severely.

Surficial Geology

The U.S. Geological Survey, Water Resources Division, was requested by the U.S. Atomic Energy Commission to provide a detailed geologic map of the Walker Branch basin to be used in planning studies of the groundwater hydrology of the basin. The Walker Branch basin is underlain by the Knox group, a

WALKER BRANCH WATERSHED

1967 BURN -

Fig. 2.28. Aerial extent of two fires which burned on Walker Branch watershed during 1967 superimposed on 1967 photograph of the area.

2000-ft-thick sequence of siliceous dolomite, divided into four formations on the basis of minor variations in lithology and chert characteristics. Approximate contacts between formations are shown in Fig. 2.21, and stratigraphic sequence, thicknesses, and general characteristics are summarized in Table 2.6. Bedding planes in the rocks generally strike N60E, and dip is 30 to 40° to the southeast. Although it is likely that minor structural anomalies exist in the basin as small folds or faults, no evidence of such was observed in adjacent basins. Two prominent sets of joints were observed, one striking about N55W and the other nearly east-west.

The bedrock geology is largely obscured by a mantle of weathering products from the underlying dolomite and is thickest along drainage divides. Chert is interspersed throughout the weathered mantle but is concentrated at the ground surface and bedrock-weathered material interface. Depth to bedrock is highly variable.

The mass of weathered material probably is the major groundwater reservoir of the basin. The directions of lateral water movement in the weathered material are closely related to surface topography. Any water moving through the bedrock should be expected to be confined to openings along joints and bedding planes which range in size from very small (most numerous) to cave-size openings (limited areal occurrence). Direction of water movement in solution openings generally conforms to surface topography, but may have no apparent relation to present topography. Extensive solution openings in the bedrock of Walker Branch basin and their approximate areal extent are shown in Fig. 2.21. The exact number of sinkholes contributing water to the Walker Branch drainage area is unknown. Sinkholes along the northwestern divide are probably

tributary, while sinkholes along the northeastern and southwestern divides probably are not tributary to Walker Branch, since solution openings in tilted carbonate rocks generally develop lengthwise along bedding planes or parallel to strike.

Based on examination of the basic geology, both topography and geologic structure are favorable for water movement from East to West Fork. The survey further indicated that such a transfer may occur in a 1000-ft reach along the East Fork with the central point of the reach at the base of the Longview formation (Fig. 2.21). If water transfer between forks occurs, water would be expected to move along the strike to be discharged to the West Fork. Even though valley alluvium and slope wash deposits which are water storage reservoirs are more extensive in the valley of the East Fork, base flow discharges are better sustained from the West Fork than the East Fork. If lateral water transfer from East to West Fork is not significant, higher base flows would imply that storage capacity of West Fork basin is greater than in the East Fork basin. Storage capacity can be compared using unit-area flood volumes for each basin. If unit-area flood volume from the West basin is smaller than from the East, the West basin would be storing more water for release later, thus resulting in higher sustained base flows. Storage difference would be reflected in a comparison of flood volumes discharged from each basin. Unit-area flood volumes would be larger from East Fork basin, and reflect its lower storage capacity. In fact, unit-area flood discharge is from 1.3 to 1.8 times greater from the West Fork basin than from the East basin, thus indicating: (1) that lateral flow from East to West is significant and/or (2) that the storage capacity of the East basin is greater.

Table 2.6. Characteristics of geologic formations underlying Walker Branch basin

System	Series	Group	Formation	Thickness (m)	Description
Ordovician	Lower Ordovician	Knox	Newah	335	(Follow description on map)
		Knox	Longview Dolomite	122	
		Knox	Chaptalia Dolomite	168	
Cambrian	Upper Cambrian	Knox	Copper Ridge Dolomite	385	

SYSTEM	SERIES	GROUP	FORMATION	LITHOLOGY	THICKNESS IN FEET (APPROX.)	DESCRIPTION
ORDOVICIAN	LOWER ORDOVICIAN	KNOX	NEWALA FORMATION		1100	UPPER PART IS DOLOMITE, LIGHT GRAY, VERY FINELY CRYSTALLINE, SILICEOUS, MOSTLY IN BEDS 2 TO 4 FEET THICK. OUTCROP AREA OF UPPER PART IS OUTSIDE WALKER BRANCH BASIN ALONG SOUTHEAST SLOPES OF SOUTH-EAST DRAINAGE DIVIDE. LOWER PART IS DOLOMITE, LIGHT GRAY, COMMONLY CONTAINING ABUNDANT MAROON AND GREENISH MOTTLED, FINELY CRYSTALLINE, ABUNDANT JASPER CHERT IN NODULES AND LAYERS AND ON GROUND SURFACE. A FEW THIN BEDS OF OLIVE-GRAY LIMESTONE. WEATHERED MATERIAL OVER BEDROCK APPEARS TO BE THINNER THAN OVER OTHER FORMATIONS IN BASIN AND OUTCROPS ARE COMMON.
			LONGVIEW DOLOMITE		400	DOLOMITE, LIGHT GRAY TO GRAY-TAN FINELY TO COARSELY CRYSTALLINE, VERY SILICEOUS. ABUNDANT CHERT (WEATHERED) MATERIAL IS GENERALLY LIGHT-COLORED, DENSE, ANGULAR. CHERT OCCURS IN BLOCKS, LOCALLY OF LARGE SIZE. WEATHERED MATERIAL APPEARS TO BE FAIRLY THICK AND OUTCROPS ARE SPARSE.
			CHEPULTEPEC DOLOMITE		550	DOLOMITE, LIGHT GRAY FINELY TO MEDIUM CRYSTALLINE, LESS SILICEOUS THAN OTHER FORMATIONS IN WALKER BRANCH BASIN, BUT LOCAL CHERT CONCENTRATIONS OCCUR ON GROUND SURFACE. CHERT MOSTLY LIGHT GRAY, POROUS OR CAVERNOUS, ROUNDED SURFACES, AND CONTAINS SMALL WHITE OOLITES. PRESENCE OF SANDSTONE BEDS IN LOWER PART INDICATED BY 3- TO 6-INCH THICK BLOCKS OF LIGHT-BROWN SANDSTONE FLOAT. WEATHERED MATERIALS ARE FAIRLY THICK AND OUTCROPS ARE VERY FEW.
		CAMBRIAN	UPPER CAMBRIAN	COPPER RIDGE DOLOMITE	1000	DOLOMITE, MEDIUM TO DARK GRAY, COARSELY CRYSTALLINE, ASPHALTIC, VERY SILICEOUS. DOES NOT CROP OUT IN WALKER BRANCH BASIN. RESIDUAL CHERT IS TYPICALLY LIGHT TO MEDIUM GRAY, DENSE, AND CONTAINS PROMINENT BANDED OOLITES. WEATHERED MATERIALS APPEAR TO BE THICK.

Fig. 2.21. Topographic map of Walker Branch watershed showing bedrock types and approximate boundaries. Walker Branch are outlined. Mapping was done using aerial photographs at a scale of 1 in. to 264 ft and a 10-ft contour.

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ORNL-DWG 72-27'A

Approximate boundaries Sinkhole depressions that possibly are tributary to Walker and a 10-ft contour interval map.

2

3. International Biological Program: Oak Ridge Research Site

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Land-water interactions, and their governing ecological components and processes, are the delicate balances which must be understood as man continues to manipulate his environment. The Oak Ridge site of the U.S. IBP Eastern Deciduous Forest Biome proposes as its unique contribution the study of land-water interactions based on a research program executed at three hierarchical levels of organization. Simultaneous development at the level of processes and components of specific ecosystems permits evaluation of the significance of these processes and consequences of their modification and alteration to system behavior. Information on the basic production processes which regulate forest ecosystems is being obtained to provide comparative data on the efficiencies of alternative choices of land use in terms of solar energy conversion, biomass production, and mineral utilization. Rates of transfer of energy and materials among the components of these systems are being identified and quantified. Emphasis is being placed on the concomitant development of (1) mechanistic process models (e.g., photosynthesis, nitrogen, mineralization), (2) the coupling of process models leading to construction of dynamic stand models (ecosystem models of carbon, water, and

nutrient elements), and (3) the integration of stand models for the development of predictive models of watersheds. It is expected that significant scientific contributions in basic research and systems modeling will be made at each of the three hierarchical levels, although the integrated site research program is designed and managed to ensure the maximum degree of synthesis of all contributions into integrated ecosystem analyses.

GASEOUS EXCHANGE, FOREST CANOPY, AND METEOROLOGY

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Assessment of primary production at the Oak Ridge site consists of intensive study of physiological processes as well as investigations into net accumulation of biomass. Ultimately it is our desire to have the capability for predicting production rates for large land areas by means of a model capable of integrating environmental influences and biotic variables over time. To this end, a hierarchy of mechanistic process models is currently being developed. These models deal with plant physiological processes as they pertain to photosynthesis and primary production in general.

Photosynthesis, of all aspects of plant metabolism, shows the greatest variation under the typical regimes

-
1. Dual capacity.
 2. IBP-research assistant, UT Graduate Program in Ecology.
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of environmental microclimate. Much of our work during the past year has been directed toward development and implementation of methods for in situ analysis of photosynthesis rates in response to natural environmental fluctuation. Summaries of research results concerning primary production processes are confined to the *Liriodendron tulipifera* forest, a site for which several types of data are already available. Within this study area, we have interfaced the research efforts of forest meteorology and detailed process research.

This year's report reviews the status of studies involving canopy leaf area, phenology of photosynthetic pigments, solar radiation profiles within the canopy, and net photosynthesis and respiration rates for in situ specimens of *L. tulipifera*. An attempt was also made toward prediction of gross primary production of tulip poplar, based upon carbon dioxide fluxes.

Seasonal Dynamics of Canopy Development and Spatial and Temporal Distribution of Solar Energy in a Forest Ecosystem

Objectives of this project were definition of the seasonal development of photosynthetic surface and associated solar energy distribution within a closed-canopy deciduous forest site. Accurate and precise information with respect to amounts and distribution of foliar surface is requisite for reliable estimation of the primary productivity of forested ecosystems.

Foliage collections were made at various heights and locations within the canopies of selected yellow poplars (*Liriodendron tulipifera*) at various times during the growing season. The basic sampling unit consisted of a $\frac{1}{8}$ -m³ frame which was positioned by means of a mobile lift truck. Leaves encompassed by the sampling frame were harvested and utilized for determination of leaf area, foliage dry weight, and canopy volume, as well as for analyses of photosynthetic pigment concentration and estimates of insect consumption. Leaf area (m² leaf surface/m³ canopy volume) values were derived for the various sample dates and are plotted along with total chlorophyll concentration per unit leaf area in order to illustrate the seasonal generation of photosynthetic surface (Fig. 3.1). Allometric equations relating leaf dry weight and the product of maximum blade length and width to total surface area were derived. For estimation of foliar surface areas encompassed by the polyfilm chambers employed in gaseous exchange analyses, an equation of the form

$$Y = 1.278X + 0.179 \quad (1)$$

Fig. 3.1. Seasonal patterns of leaf surface per unit canopy volume and total chlorophyll concentration per unit leaf surface.

Table 3.1. Summary of canopy parameters for three *Liriodendron tulipifera* harvested during August 1971

Sample date	Tree height (m)	Diameter breast height (cm)	Leaf weight (kg)	Leaf area (m ²)	Leaf area index (m ² /m ²)
8/20	24.3	22.9	4.90	54.3	6.68
8/25	21.6	20.1	2.86	39.3	5.41
8/26	25.9	29.7	4.91	58.3	6.16

was used, wherein X = dry weight of leaves in grams and Y = surface area in square decimeters.

In conjunction with sampling portions of the canopy, three yellow poplar trees were harvested at maximum canopy development. Canopy and main stem dimensions were determined for these, along with measurements of leaf and branch angle and orientation. Total canopy surface and leaf area index (LAI) values were derived allometrically (Table 3.1).

Leaf area values (m² leaf surface/m³ canopy volume) as estimated from canopy samples exhibit a typical sigmoidal development curve with maximum values being reached during the first week in June, a period which approximates the 10th week of foliar development (Fig. 3.1). Maximal photosynthetic surface area is reached early in the season, and does not appear to decrease appreciably over the measured interval.

Leaf surface data obtained by harvesting entire trees yielded a mean LAI value of 6.1 m² leaf surface/m² ground area under canopy (Table 3.1). Leaf surface-ground area ratios generally range from 4.0 to 6.0 m²/m² for closed canopy deciduous forests; thus,

results of harvesting do not appear to be at variance with expected values.⁷

Total chlorophyll concentrations per unit of leaf area exhibit a similar relationship with time as does foliar surface development (Fig. 3.1). Chlorophyll concentrations equivalent to 3.0 to 3.5 $\mu\text{g}/\text{cm}^2$ of leaf surface prevail over most of the growing period.

Maximum leaf numbers per unit canopy volume are reached early in the season (Fig. 3.2). Estimates of insect consumption follow the same general trend with equilibrium between production and consumption occurring during the latter portion of the growing season. Total annual insect consumption accounts for approximately 3% of net foliar area.

The distribution and variation in intensity of solar radiation within the forest canopy were monitored during relatively cloud-free days to evaluate the effects of canopy development upon the spatial distribution of light. Lintronic dome solarimeters, sensitive over a range 0.3 to 3.0 μ , were located at random: on the forest floor (17 open + 3 shaded), and nonrandom positions within mid (3 open + 2 shaded) and upper (3 open + 2 shaded) portions of the canopy. Shadow bands were employed to allow separation of total incident radiation into the direct beam and diffuse components by subtraction of values obtained from sensors equipped with shadow bands from total radiation received by the nonshaded sensors. Data presented were obtained during spring 1969 and are considered as being representative of conditions within the *Liriodenaron* site over the interval of foliar development (Fig. 3.3). Comparison of direct beam intensities measured in the upper canopy with those measured at ground level reveals that during early stages of foliar development some 70% of incoming radiation is blocked by foliage. As canopy development progresses, nearly 94% of the direct beam component is intercepted. Ratios of upper canopy to lower canopy direct beam components exhibit a transitory increase over the measured interval, and would be expected to remain relatively constant following full canopy development.

The overall dynamics of canopy development appear to be one of early maximization of photosynthetic surface and associated photopigment concentrations which remain stable throughout the growing season. Information as to both the phenology of canopy development, as well as quantitative measures of canopy phenology, surface area relationships, and pigment concentrations are prerequisite for development of

models describing productivity of deciduous forest stands. Knowledge of foliar distribution and penetration and interception of solar radiation is necessary to predict photosynthetic efficiency. The coupling of these predictions with mechanistic representations of actual physiological processes will then allow estimation of actual energy conversion and associated biomass accumulation.

Gaseous Exchange Apparatus for in Situ Photosynthesis Studies

In studies of photosynthesis, modern techniques of plant ecophysiology consist of measurement of the carbon dioxide flux of the intact plant, or portions thereof, by means of sensitive instruments for quantitative gas-stream analysis. Changes in CO_2 concentration of an artificially produced airstream which is passed through a chamber containing the aerial portions of the plant are monitored through utilization of an infrared gas analyzer. These methods unavoidably alter the microenvironment of the shoot, resulting in somewhat limited results. However, they do allow some degree of control of microclimatological variables, thus permitting studies of plant response to changes in levels of these variables.

The apparatus described below was designed to provide a sensitive, versatile tool for in situ studies of physiological and environmental control of carbon dioxide exchange between plant and atmosphere (Fig. 3.4). The system is of the open type wherein the chamber is continuously purged and plant-induced changes in airstream composition are determined by analysis of incoming and outgoing air. Chambers of this type are suitable for most ecological investigations,

Fig. 3.2. Seasonal patterns of mean numbers of leaves per unit canopy volume and estimated percent canopy consumption.

7. R. H. Whittaker and G. M. Woodwell, *Amer. J. Bot.* 54, 931-39 (1967).

Fig. 3.3. Average radiation intensities in a *Liriodendron* forest for the period solar noon $\pm$ 3 hr.

except for those which require exact duplications of the natural microenvironment.

The plant chamber consists of a polyfilm bag fastened to a heat exchanger. Portions of the plant are enclosed within the bag, the neck of which is sealed at the base of the stem with Duxseal and a dacron tie. The heat exchanger is fitted with a movable face plate to permit rapid replacement of the polyethylene bag. Inlet and outlet tubes are provided for both cooling water and the chamber air stream. Conduits allow insertion of thermocouple and electrical leads into the chamber. Air turbulence within the chamber is provided by a multibladed fan connected in series with a rheostat.

Temperature control within the plant chamber is effected by circulating thermostatically controlled cool water through the coils of the heat exchangers. Thermally activated proportional solenoid valves (PSV) allow for selection and maintenance of controlled chamber temperatures over the range 15 to 35°C. Copper-constantan thermocouples inserted within and adjacent to the plant chamber monitor ambient and chamber temperatures. Temperatures of enclosed leaves

are determined by means of microthermocouples epoxied to the leaf surfaces. Incident solar radiation (0.3 to 3.0 μ) levels are monitored by means of domed solarimeters attached to the heat exchanger brackets. Atmospheric vapor pressure deficits are calculated from wet and dry psychrometer temperatures.

Air is supplied to the chamber by means of a membrane pump (Pa) and stream selector assembly. The pressure side of the pump feeds four branch lines, two of which lead to the plant chambers and subsequently to the infrared gas analyzer (IRGA), and two of which flow at constant rates through the IRGA, serving as references for ambient CO₂ concentration determinations. Flowmeter (FM) assemblies are installed in the various tubes as indicated. The addition of a drying column (DEC) serves to prevent water vapor from entering the analyzer. Planned modifications include the addition of a trace moisture analyzer for measurement of plant water vapor exchange.

Net photosynthesis and respiration are determined as a function of the product of the difference (Δ CO₂) between concentration of the airstream entering and

that leaving the plant chamber and flow rate through the chamber. Gas laws and mass-volume relationships allow the expression of this product in terms of actual weight of CO_2 per unit time. Surface areas, as well as fresh and dry weight of plant samples, are determined, allowing the expression of carbon dioxide flux as rate per unit time per unit area, or unit weight of photosynthetic tissue.

Data obtained in field tests of the apparatus are shown in Fig. 3.5. A comparison of ambient and chamber temperatures over the range 10 to 35°C reveals that chamber temperatures generally lie within -1 to $+3^\circ\text{C}$ of ambient levels (Fig. 3.5a). Leaf temperatures may also remain very close to chamber air temperatures, except at high-temperature levels brought about by increased amounts of solar radiation (Fig. 3.5b).

Chamber-ambient and leaf-chamber temperature differentials may be noted to vary directly with increased amounts of incident radiation (Fig. 3.5c and 3.5d). This phenomenon is due to absorption and conversion of shorter wavelengths of incident sunlight to longer or thermal radiation. Leaf-chamber temperature differentials remained within -2 to $+6^\circ\text{C}$ of chamber tempera-

ture, preventing thermal injury to the leaves, a common occurrence in nonregulated chambers.

A sample calculation of CO_2 flux is as follows:

$$P_n = 115 \text{ ppm} \times 1.97694 \text{ g/liter (density of } \text{CCl}_2\text{)}$$

$$\times \frac{P}{T} \times \frac{273}{760} (\text{NTP}) \times 10^{-6} = \text{g/liter} \quad (2)$$

$$P_n = 115 \times \frac{P}{T + 273} \times 7.101 \times 10^{-7} = \text{g/liter} \quad (3)$$

$$P_n = 115 \times \frac{740}{323} \times 7.101$$

$$\times 10^{-7} = 1.871 \times 10^{-1} \text{ mg/liter} \quad (4)$$

$$P_n \times FR \times \frac{1}{SA} = 1.871 \times 10^{-1} \times 720 \text{ liters/hr}$$

$$\times \frac{1}{30.15 \text{ dm}^2} = 4.468 \text{ mg dm}^{-2} \text{ hr}^{-1} \quad (5)$$

ORNL-DWG 72-258

Fig. 3.4. Diagram of gaseous exchange apparatus.

Fig. 3.5. Data obtained in tests of the apparatus showing: (A) relationship between plant chamber and ambient air temperatures; (B) relationship between leaf temperature and chamber temperature; (C) comparison of chamber-ambient temperature differentials over a range of light intensities; and (D) comparison of leaf-chamber temperature differentials over a range of light intensities.

where

$CC_2 = -115 \text{ ppm} = \text{net photosynthesis (Pn)},$

$FR = 720 \text{ liters/hr} = \text{flow rate},$

$T = 50^\circ\text{C} = \text{analyzer sample cell temperature},$

$P = 740 \text{ mm Hg} = \text{barometric pressure},$

$SA = 30.15 \text{ dm}^2 = \text{foliar surface area}.$

Net Photosynthesis and Annual Productivity of *Liriodendron tulipifera* Estimated from Carbon Dioxide Exchange

Measurements of carbon dioxide exchange within the canopy of the *Liriodendron tulipifera* forest study site were carried out during the later portion of the growing season by means of the apparatus described previously. Net photosynthesis of yellow poplar as a function of light intensity is shown in Fig. 3.6. Maximum net photosynthetic rates approaching 5.0 to 5.2 mg dm⁻² hr⁻¹ were attained at light intensities $\geq 0.42 \text{ cal cm}^{-2}$

min⁻¹ (2950 ft-c). Yellow poplar is considered as shade-intolerant, a fact which is supported by the high light intensities necessary for light saturation. Light requirements have been measured for a number of other forest species, and have been found to vary considerably. Specimens of shade-tolerant *Acer saccharum* were found to be light-saturated at 0.07 cal cm⁻² min⁻¹ (800 ft-c); *Quercus velutina*, an extremely shade-intolerant species, was light-saturated at 3200 ft-c.⁸

Maximum rates of net photosynthesis for portions of the *Liriodendron* canopy were approximately 6.5 mg dm⁻² hr⁻¹ at optimum temperatures and light levels (Fig. 3.7). The temperature dependence of net photosynthesis is apparent in that at higher light intensities temperature optima were noted to shift toward greater values. Increased temperatures at subsaturation light

8. J. E. Wuenschel and T. T. Kozlowski. *Can. J. Bot.* 48, 453-56 (1970).

Fig. 3.6. Relationship of net photosynthesis to light intensity for in situ measurements of *Liriodendron tulipifera* at 25°C. Flow rates through the chambers were maintained at 12 liters/min to prevent depletion of CO₂ in the chamber. Incoming CO₂ content ranged from 300 to 325 ppm. Leaf and air temperatures were measured with copper-constantan thermocouples.

Fig. 3.7. Relationship between net photosynthesis rates and leaf temperature at various light intensities.

intensities (i.e., $<0.42 \text{ cal cm}^{-2} \text{ min}^{-1}$) are accompanied by elevated respiratory rates which are not compensated by increased CO₂ fixation as occurs at higher light intensities.

Net photosynthesis rates at light intensities $>0.42 \text{ cal cm}^{-2} \text{ min}^{-1}$ exhibit temperature optima over a range 26 to 30°C (Fig. 3.7). These rates probably reflect a preponderance of sun leaves, but are in accordance with temperature requirements observed for other species. Schulze⁹ observed temperature optima for in situ net photosynthesis of *Fagus sylvatica* to range from 10 to 30°C over the season.

Data from a 24-hr period of continuous measurement of CO₂ flux (August 14–15, 1971) were used for preliminary extrapolation to an annual production balance. This estimate is based upon a 180-day season and litterfall biomass data (Table 3.2). Daytime rates of CO₂ uptake ($45.73 \text{ mg CO}_2 \text{ g}^{-1} \text{ day}^{-1}$) less nighttime respiration rates ($6.01 \text{ mg CO}_2 \text{ g}^{-1} \text{ day}^{-1}$) equal a net seasonal CO₂ uptake of 7.15 g of CO₂ per g of foliage, or 1501.5 g of CO₂ per m² of net CO₂ uptake per season ($\text{g/m}^2 \text{ foliage} \times \text{g CO}_2 \text{ uptake/g foliage}$). An approximation of the weight of carbohydrate produced is obtained by using the conversion factor 0.614 g of carbohydrate per g of CO₂.¹⁰ Thus, annual net carbohydrate production of *Liriodendron tulipifera* becomes 0.92 kg/m² ($1.5015 \text{ kg CO}_2 \text{ uptake per m}^2 \times 0.614$).

A lower bound on gross production can be approximated by assuming that daytime respiration is equivalent to nighttime rates and adding the latter to daytime CO₂ uptake. This procedure neglects photorespiration, a phenomenon which cannot be measured satisfactorily under forced conditions. Addition of dark respiration rates and adjusting for carbohydrate production gives an estimate of gross annual primary production for *Liriodendron tulipifera* of 1.20 kg of carbohydrate per m².

9. E. D. Schulze, *Flora*, Bd. 159, S. 177–232 (1970).

10. D. B. Botkin et al., *Ecology* 51, 1057–60 (1970).

Table 3.2. Net carbon dioxide uptake for in situ specimens of *Liriodendron*, August 14–15, 1971

Leaves/area (g/m ²)	Daytime CO ₂ uptake		24-hr CO ₂ uptake		Dark respiration	
	Per leaf (g/g)	Per area (g/m ²)	Per leaf (g/g)	Per area (g/m ²)	Per leaf (g/g)	Per area (g/m ²)
210.0	8.23	1728.3	7.15	1501.5	1.08	226.8

While these values are based upon limited CO₂ fixation data, the estimate of gross productivity approaches estimates for other deciduous forest species (*Quercus coccinea* gross annual productivity of 1.10 kg of carbohydrate per m²).¹⁹ As more data become available, including seasonal variations in CO₂ flux for tulip poplar and associated major biomass components, a more refined estimate of gross primary production for this forest may be realized.

TERRESTRIAL PRIMARY PRODUCTION

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The objectives of terrestrial primary production studies at the Oak Ridge site are the development and validation of models describing the dynamics of forested ecosystems at three levels of resolution: canopy structure and basic physiological processes (see Gaseous Exchange – Forest Canopy Meteorology), discrete portions of forested landscapes, and larger units with clear topographic boundaries such as forested watersheds. By approaching terrestrial primary production at three levels simultaneously, results of data synthesis can be applied not only to questions concerning process efficiency under stress, but also questions directed toward accumulation and subsequent turnover of trophic levels over large geographic areas. With concurrent development of data bases and conceptual models at the different levels of process resolution, an increased amount of feedback between physiological and stand model development can be realized. For example, estimates of stand leaf area and its distribution in time and space will facilitate extension of results from gas exchange studies with branches and seedlings to entire forest canopies. On the other hand, knowledge of actual process rates and seasonal distribution of environmental conditions in the canopy is being used to develop a stand growth model which will be less empirical and more correlative with actual physiological process phenomena. This year's report reviews the status of studies on the relationship of phenology to net production of the herbaceous component of the forest; development of a general allometric model for prediction of tree biomass by major component (bole, branch, and foliage); the status of belowground biomass determination; and forest stand net production on one type of successional series. A first-generation stand model is discussed as a sum-

mary of our present state-of-the-art with an emphasis on the direction of future primary production research relative to our objectives.

Relationship of Phenology to Productivity of Herbaceous Plants

During the life cycle of a species, plants undergo a series of distinct, genetically determined life forms. These forms or phenophases are controlled by environmental factors, and consequently correspond to seasonal fluctuations. The life forms or phenophases begin with seed germination, progress through vegetative and reproductive cycles, and terminate in senescence and leaf drop. Associated with the phenodynamics are changes in biomass, productivity, and nutrient composition. Such quantitative analyses reflect the interaction of meteorology with primary production and mineral cycling in forest ecosystems. The relationship of phenology to primary production and nutrient composition in forest ecosystems, dominated by *Liriodendron tulipifera*, is being assessed for understory and herbaceous species (*Cornus florida*, *Hydrangea arborescens*, *Podophyllum peltatum*, *Polystichum acrostichoides*). An example of the kinds of analyses being made for each species is illustrated by biomass and productivity estimates in mayapple, *Podophyllum*.

Mayapple, because of its social occurrence and rapid phenological development in spring, is one of the most conspicuous herbaceous species of eastern deciduous forests. Emerging from the soil before the last killing frost (April 15), mayapple completes its life cycle by midsummer (August 26). Within the *Liriodendron* forest study area the species is best established in social communities on low, moist sites. Being partially clonal with moderate longevity, the perennial communities vary in area from 0.7 to 176.6 m², appearing elliptical to orbicular in shape (Fig. 3.8). The species has a well-developed, over-wintering, underground rhizome-root system. The aerial leaves within a community, analogous to individual plants, exhibit simultaneous phenological development due to the clonal nature of the species. Within the forests adjacent to the *Liriodendron* site, diameters of 21 mayapple communities were measured and the number of aerial plants determined. Regression analysis of computed area to number of plants resulted in a correlation coefficient ($r = 0.94$). From the resulting regression (Fig. 3.9), the number of aerial plants can be estimated if the area of the community is known.

Beginning with leaf emergence (yearday 99), 20 aerial plants were harvested at each of 8 life phases. Plants

Fig. 3.8. Typical community of mayapple (*Podophyllum peltatum* L.) in the *Liriodendron* forest study area.

Fig. 3.9. Relationship between number of aerial plants and community size (m^2) in mayapple. Data points represent communities from 0.66 to 176.6 m^2 , containing from 10 to 683 plants. The average community was 21.04 m^2 , while the average number of aerial plants was 167.24.

were compartmentalized into leaf, stem, flower or fruit, and rhizome-root for biomass estimates. Estimates of rhizome-root biomass during the leaf emergence phase (yearday 99 to 102) were considered standing crop, such that subsequent rhizome-root estimates would reflect changes throughout the life cycle. Biomass

increased for each component with the progression of the life cycle (Fig. 3.10), reaching maximum dry weight during the phase of unripe seeds and fruits prior to onset of senescence (yearday 162). At that point rhizome-root showed an increase of 21% in dry weight above the standing crop estimate during leaf emergence. Leaf and stem (petiole) accounted for 57%, whereas unripe fruit and seeds accounted for 17% of dry weight. The underground rhizome system grows terminally, producing an overwintering apical meristem. Growth is initiated during the flowering phase (yearday 116 to 123), and showed an increase of 4% in dry weight prior to senescence of aerial plants. At the onset of senescence (yearday 162), leaves begin to change color, followed by leaf and fruit drop and subsequent decreases in dry weight. Further increases in the current increment to the rhizome-root system (1971) were accompanied by decreases in dry weight of the previous increment (1970), indicating that the rhizome functions as a storage organ for growth demands. By the end of the life cycle (yearday 240), each increment in rhizome-root (1970 and 1971) accounted for 25% of the biomass. Biomass is summarized (Fig. 3.11) per individual plant. A typical mayapple community is defined as the average mayapple community within the *Liriodendron* forest study site [area = 21.04 $\text{m}^2 \pm 8.69$ (SE), number of aerial plants 167 ± 42.6]. Based on frequency of mayapple in sample plots (70%) and standard community parameters, mayapple annual pro-

duction for the *Liriodendron* forest study area was 7.0 g/m^2 aboveground and 1.5 g/m^2 belowground.

Productivity estimates per unit forest area (Fig. 3.11) reflect growth above the standing crop of rhizome-root at leaf emergence. During leaf emergence the rate of dry matter productivity per plant is $0.2 \text{ g m}^{-2} \text{ day}^{-1}$ ($0.17 \text{ g plant}^{-1} \text{ day}^{-1}$). Productivity is maximum during the onset of the reproductive phase, yearday 103 to 116

($0.53 \text{ g m}^{-2} \text{ day}^{-1}$), declining rapidly through flowering and fruiting phases. The decrease in production between yearday 163 and day 181 (0.10 to $0.03 \text{ g plant}^{-1} \text{ day}^{-1}$) represents a loss due to consumption of ripe fruits by small mammals and insects. As indicated in biomass data, unripe and ripe fruits represent 17% of the total dry weight. By the end of the life cycle production, mainly limited to the 1971 rhizome sys-

Fig. 3.10. Biomass in mayapple, partitioned into obvious components. Phenophases correspond to the following time intervals: Yeardays 99–102 (leaf emergence), 102–103 (leaves opening), 99–116 (flower buds), 116–123 (flowering), 123–178 (unripe fruits, seeds), 178–196 and 196–240 (leaf drop and seed dispersal). The vegetative or growth phase is between yearday 99 to 162. Color change (senescence) of leaves begins on yearday 162 and terminates with total leaf drop, day 240.

Fig. 3.11. Seasonal productivity by mayapple, *Podophyllum peltatum*.

Table 3.3. Summary by species group (numbers of harvested trees in each size class) following TVA code of diameter distribution (DBH) of tree harvest data contributions to the central harvest data file

Data on 40 species of woody shrubs and trees, including 250 trees >10 cm in DBH, have been located.

Group	Total No. trees	Diameter class (cm DBH)						
		<1	<5	<10	<15	<20	<30	>30
Pines	98	51	36	3	7	1	0	0
Hemlock-spruce	18	0	0	6	1	3	1	7
Oaks	173	116	5	6	13	9	7	17
Soft hardwoods	259	174	28	14	12	8	8	15
Hard hardwoods	313	187	61	23	10	9	12	11
Post species	40	33	1	4	1	1	0	0
Noncommercial trees and shrubs	123	62	28	22	3	2	5	1
Total	1024	623	159	78	47	33	33	51

tem, had decreased to $0.03 \text{ g m}^{-2} \text{ day}^{-1}$ ($0.025 \text{ g plant}^{-1} \text{ day}^{-1}$).

These results illustrate the relationship of short-termed phenological events of species to productivity estimates, and inputs to litter and subsequent mineral cycling processes in forest ecosystems. Further analyses will determine nutrient composition and fluxes as related to phenological events.

Forest Stand Production

Estimates of net primary production for forest stands presently are based on remeasurement of diameter distributions on permanent plots, relating diameter to weight and surface area allometrically. Forest stand inventory data have been collected both locally and for forest types and site conditions representative of major deciduous forest formations.¹¹ Results from numerous projects has been summarized in order to develop a large harvest data base¹² to be used to derive a set of general allometric relationships (Table 3.3). The collection and analysis of this data base provide a degree of commonality in data analysis across site and biome projects heretofore impossible to attain.

Several regression models have been used to develop allometric relationships of weight and surface area of trees. The most common model in the literature is the power function

$$\hat{Y} = aX^b, \quad (6)$$

where $\hat{Y}$ is the biomass component (e.g., bole, branch, or foliage biomass), X is the independent variable (diameter breast height), and a and b are regression constants. Estimating equations of this form usually use a logarithmic transformation to produce a linear form:

$$\ln \hat{Y} = a + b \ln X. \quad (7)$$

Transformation back to the original units results in the allometric relation

$$\hat{Y} = e^a X^b. \quad (8)$$

Regression coefficients for major tree groups (hardwood, conifers, and all combined) are summarized in Table 3.4. Regardless of the heterogeneity of sites and species characteristics represented in the data base, consistent relationships exist between various biomass components and DBH.

The retransformation of logarithmic regression parameters introduces bias into estimates of Y in that the logarithmic transformation of weight results in an estimate of the geometric, rather than arithmetic, mean weight of trees in a given diameter class. The geometric mean usually underestimates the arithmetic mean, the degree of bias being affected by the variance of the weight data. A procedure was developed for estimating the magnitude of this bias based on earlier work by Finney.^{13,14} Table 3.4 summarizes the correction factor (K) applicable to bole, branch, and foliage weight for the "all species" regression model. Figure 3.12

11. Both the Tennessee Valley Authority and U.S. Forest Service have provided access to continuous forest inventory plot data.

12. P. Sollins and R. Anderson, ORNL-IBP-71-6 (1971).

13. D. J. Finney, *JRSS Suppl.* 7, 155-61 (1941).

14. J. Beauchamp and J. S. Olson, manuscript submitted to *Biometrika*.

Table 3.4. Summary of uncorrected regressions (ln-1a) of tree component weight (kg) on tree diameter breast height (cm)

Dependent variable		Intercept (a)	Slope (b)	Coefficient of determination (R^2)	Sample size (N)	K^a
Leaf	All species	-3.498	1.695	0.86	302	1.34
	Hardwoods	-3.862	1.740	0.88	178	
	Conifers	-2.907	1.674	0.91	65	
Branch	All species	-3.188	2.226	0.91	298	1.26
	Hardwoods	-3.173	2.224	0.89	231	
	Conifers	-3.461	2.292	0.95	51	
Bolt	All species	-2.457	2.418	0.97	298	1.08
	Hardwoods	-2.270	2.385	0.98	231	
	Conifers	-3.787	2.767	0.96	51	
Branch-bolt	All species	-2.126	2.393	0.96	371	
	Hardwoods					
	Conifers					

^a K = multiplying factor used to adjust $\hat{Y}$.

shows the effect of K on regression estimates of components of tree biomass. We are currently using the all species regression coefficients and associated K values to estimate stand biomass (see Walker Branch watershed project; and Regional Studies, this report).

Root Biomass Dynamics

Accurate estimates of belowground standing biomass, production, and turnover are essential to ecosystem analysis because roots comprise at least 20 to 25% of total organic material in terrestrial ecosystems. Moreover, their role in ecosystem physiology of mineral and water cycling and as a substrate for decomposers must be clearly defined. Research initiated this year has developed estimates of forest stand root biomass on a seasonal basis. Since the excavation of entire root systems is impractical, allometric relations of stump and butt roots to diameter breast height are being developed from stumps of uprooted trees from local logging operations. Lateral root biomass is determined from excavation of 0.25 m² soil pits where soils are shallow with high stone content (e.g., Walker Branch watershed project) or coring with a power corer adapted from a masonry hole saw in stone-free soils. Lateral root biomass per unit area will be related to stand basal area or aboveground biomass.

Lateral root biomass estimates for the *Liriodendron tulipifera* forest study area are summarized in Fig. 3.13. At all dates during the season, at least 60% of the root biomass was found in the 0- to 20-cm zone. The

fluctuation of root biomass with depth may reflect seasonal environmental influences or intrinsic variance in distribution. The apparent decrease in root between April and June may reflect translocation of carbohydrate to the aboveground plant parts. Root production for both size classes considered began after June 15 and continued into the early fall. Samples of root biomass are being analyzed for mineral and carbohydrate content in order to determine the magnitude of vernal mineral and carbohydrate flux upward. The mean standing lateral root biomass was 2.21 kg/m² with a difference of 1.70 kg/m² between June and September values; this indicates a high apparent net root productivity and either high rates of root mortality or translocation, or more likely both. A greenhouse study of the mineralization of yellow poplar root biomass indicates that during the period of maximum root growth 5 to 9% of the total root weight is composed of dead material. Approximately 90% of the turnover is accounted for in the roots less than 0.5 cm in diameter with approximately 75% of the total turnover in the roots less than 0.1 cm diameter.

These results have suggested several areas for further study. A project was initiated this fall to measure in situ rates of root decay and mineralization using buried root material enclosed in large mesh nylon net. This work will be replicated seasonally to estimate influences of temperature and soil moisture on these processes. A pilot study also was initiated this fall using ¹⁴C-sucrose as a stem tag. By tagging late in the growing season most of the ¹⁴C-sucrose was translocated to the root

Fig. 3.12. Regression estimators of individual tree biomass vs diameter at breast height for (a) leaf, (b) branch, and (c) bole components. The regression lines before $[\exp(\ln \hat{Y})]$ and after $[\exp(\ln \hat{Y}) \cdot K]$ application of the correction factor (K) are shown. Regressions are based on combined data for 40 tree species.

Fig. 3.13. Root biomass (g/m^2) profile with soil depth for (a) roots > 0.5 cm in diameter and (b) roots ≤ 0.5 cm in diameter in the *Liriodendron* study site. Estimates are based on 15 cores at each date with each core taken to a depth of 60 cm. Total root biomass at each date is summarized in the histogram beneath each profile.

system. The rates of $^{14}\text{CO}_2$ evolution are being monitored to estimate the rate of total organic carbon turnover, including microbial action on root exudates as well as dead root biomass. Next spring ^{14}C activity will be monitored in roots, as well as developing foliage to evaluate the influence of stored carbohydrate on current foliage development. With continued integration of studies of root biomass, turnover, and translocation, a clearer understanding of the contribution of this compartment to carbon and mineral cycles will be realized.

Species Composition and Productivity of Upland Oak Seres

Forest communities undergoing secondary succession display trends not only in composition, but also in stand productivity and biomass. Compositional changes in upland oak forest communities of the Oak Ridge Reservation are being evaluated along with the accompanying changes in productivity and stand biomass. By measuring changes in productivity of ecosystems along a successional gradient, results of process research can be coupled more effectively with successional changes in community composition and structure.

Data on species, diameter, standing dead, and growth are being collected on plots in 15 ridgetop sites. The sites are all on typic paleudult soils mostly underlain by cherty Knox dolomite. Sites with similar characteristics were chosen to minimize the effects of slope, aspect, and fertility that affect community production. Dif-

ferent stages of forest succession from almost pure pine stands to mature oak-hickory stands are included (Table 3.5). Using this data base, species importance (defined as sum of relative basal area and density) changes in basal area, density, biomass and productivity are being compared among serai communities.

Stages of early forest succession are characterized initially by low species diversity, increasing as the forest approaches climax, with dominance being shared by several species. An increase in biomass through succession sometimes accompanied by a decrease in productivity supposedly characterizes many successions.¹⁵ Data summarized in Table 3.5 illustrate these hypotheses. Young (20- to 30-year) pioneer sites dominated by shortleaf pine (*Pinus echinata*) have low biomass, high density, low basal area, and high percent increase in biomass. Transition stages between a pioneer pine stand and the climax oak stands (e.g., site 205, Table 3.5) are characterized by genera that become established beneath the pine canopy (*Oxydendron*, *Acer*, *Liriodendron*). Oaks also are established, but are not an important part of the community. The stand biomass and productivity are intermediate between the pine stands and oak-dominated stands that are approaching climax; basal area is not greatly different, but density is lower. Mature oak stands (e.g., site 203, Table 3.5) are dominated by white oak (*Quercus alba*) and black oak (*Q. velutina*). Basal area and stand biomass are highest

15. E. P. Odum, *Science* 164, 262-70 (1961).

Table 3.5. Basal area, density, standing biomass, percent change in aboveground biomass for previous five-year period (1966-71), and percent biomass in leaves for pioneer, transition, and mature stands for trees <7.6 cm DBH

Stand type	Plot number	Basal area (m ² /ha)	Density (stems/ha)	Standing biomass (kg/m ²)	Percent change in biomass (five-year period)	Percent biomass in leaves
Pioneer	207-013	21.04	940	8.98	33.00	7.30
Pioneer	207-023	29.14	1140	13.40	28.85	6.73
Pioneer	207-033	24.06	1200	9.93	24.05	6.89
Pioneer	207-043	25.87	1480	9.94	6.86 ^a	6.69
Pioneer	207-053	30.75	1620	10.75	14.19	8.58
Transition	205-011	24.77	940	13.03	16.44	4.01
Transition	205-021	23.81	860	13.42	15.30	2.77
Transition	205-033	25.71	1000	14.44	14.40	2.78
Mature	203-011	40.93	480	27.63	11.30	2.03
Mature	203-021	24.14	480	15.07	13.01	2.33
Mature	203-031	38.98	560	25.35	10.37	2.17
Mature	203-043	28.61	400	17.58	-1.99 ^a	2.20

^aMortality has resulted in a greater loss of biomass during the five-year study period than can be accounted for by production of surviving trees.

Table 3.6. The three dominant species on 12 sample plots determined by three methods: importance value (sum of relative basal area and relative density), relative biomass (species biomass/plot biomass), and relative annual productivity (species biomass production/plot biomass production)

The data are for trees >7.6 cm

	Species	Importance value	Species	Relative biomass	Species	Relative annual productivity
207-043	Shortleaf pine	60.50	Shortleaf pine	56.55	Shortleaf pine	45.09
	Sassafras	15.67	Tulip poplar	26.36	Tulip poplar	32.53
	Tulip poplar	12.79	Sassafras	9.36	Sassafras	13.27
205-011	Sourwood	28.76	Shortleaf pine	34.15	Tulip poplar	24.75
	Shortleaf pine	24.03	Tulip poplar	19.58	Red maple	22.23
	Red maple	14.55	Sourwood	16.88	Shortleaf pine	21.24
205-021	Sourwood	22.37	Black oak	34.53	Tulip poplar	33.86
	Sugar maple	22.25	Sugar maple	23.47	Sugar maple	32.32
	Black oak	19.66	Sourwood	16.89	Sourwood	12.60
203-043	Red maple	20.49	Black oak	38.13	Black oak	30.40
	Black oak	19.27	White oak	15.35	Sugar maple	20.84
	White oak	14.16	Sugar maple	14.68	White oak	14.33

of the sites listed; density and percent biomass increase are the lowest. The percentage of biomass contributed by leaves decreases from the pioneer stage to climax stages of the sero. Decrease in productivity in mature stages of succession may be a result of the relative decrease in photosynthetic tissue.

Plant communities are usually discussed in terms of the dominant species in order to differentiate one community from another. Dominance has traditionally been expressed as various combinations of relative basal area, relative density, and/or relative frequency to derive an importance value.¹⁶ However, species dominance should be expressed differently in order to be meaningful in the context of analysis of ecosystem function. For example, relative biomass (species biomass/stand biomass) can be used rather than importance value when estimating the amount of the community resources incorporated in any one species. If the community function (mineral cycling, biomass production, etc.) is of interest, then relative production (species productivity/stand productivity) should be considered. Table 3.6 summarizes differences in stand dominance depending on the definition of dominance used. On plot 207-043 shortleaf pine is the dominant species regardless of the definition used; tulip poplar is a minor species when importance value alone is considered, but contributes half the biomass as the pine and two-thirds the annual biomass change. In plots 205-011 and 205-021 species vary according to the methods of determining dominance. On plot 203-043

the dominant species determined from the importance value is not even one of the three leading dominants when determined by relative biomass or relative productivity.

Primary Production – Stand Growth Model

Using stand budget information (Figs. 3.14 and 3.15) based on first-year site research, a primary production model was constructed for a component of the *Liriodendron* forest. This model was developed as a research tool to provide a link between detailed models of primary production processes and stand growth data based on periodic remeasurement. Previous stand growth models have dealt stochastically with individual trees¹⁷ or divided the stand into age or size classes using a single function to describe growth of each class.¹⁸ Our approach differed in that initially only a uniform age class of a single species (yellow poplar of age 30 to 50 years) was considered. However, this

16. F. G. Goff, "Dynamic Relations in Wisconsin Upland Forests," Ph.D. Dissertation, University of Wisconsin, 1966.

17. D. B. Botkin, J. F. Janak, and J. R. Wallis, "The Rationale, Limitations and Assumptions of a Northeast Forest Growth Simulator," IBP Research Report RC 3183 (#14604), Thomas J. Watson Research Center, Yorktown Heights, N.Y., 1970.

18. R. A. Leary, "System Identification Principles in Studies of Forest Dynamics," U.S. Forest Service Research Paper NC-45, North Central Forest Experiment Station, St. Paul, Minnesota, 1970.

Fig. 3.14. Organic matter budget for a *Liriodendron*-dominated mesic forest ecosystem at Oak Ridge. Overview of the entire forest ecosystem showing linkages between the four major subsystems and various miscellaneous compartments. All compartment values are g dry weights per m²; all transfer and increment values are g per m² per year. Compartment increment values are shown in boxes within the compartment. Values for all compartments except leaves are for the 1965-1966 dormant season. Leaf values are peak biomass. Transfers are annual totals based on an average of the 1965 and 1966 data.

component of the vegetation was divided into four compartments: leaves, buds, metabolically active stem and root tissues (plus dissolved carbohydrates), and inactive woody tissues (Fig. 3.16). Equations were developed describing transfers of carbohydrate among these compartments as functions of time of year and temperature. It was assumed that there is no respiratory loss from inactive woody tissues. Since operationally it is often impractical to classify fine roots as to species, roots of all species may have to be combined into several size classes for the total system and equations

derived to apportion photosynthate from the various species groups to these compartments.

In this initial version of the model, two transfers were considered to be instantaneous events. Bud break (consisting of complete transfer from buds to leaves) was assumed to occur on April 1. Litterfall was treated as an instantaneous event occurring on October 1. The model is presently being modified to lose leaves based on patterns measured this season (Fig. 3.24). All other flow functions were expressed as a rate constant or expression multiplied by the source compartment (Fig.

Fig. 3.15. Organic matter budget for a *Liriodendron*-dominated mesic forest ecosystem at Oak Ridge. Detailed budget of subsystem A (yellow-poplar trees). Transfer, increment, and standing crop values for fine roots refer to the yellow-poplar portion only. All compartment values are g dry weights per m²; all transfer and increment values are g per m² per year. Compartment increment values are shown in boxes within the compartment. Values for all compartments except leaves are for the 1965–1966 dormant season. Leaf values are peak biomass. Transfers are annual totals based on an average of the 1965 and 1966 data.

Fig. 3.16. Primary producer model. Initial conditions (kg/m² dry weight of organic matter) are specified in the boxes. Rate constants or expressions (year⁻¹) with compartment by which they are multiplied are shown next to the flow arrows. Solid arrows indicate continuous flows; broken-line arrows indicate transfers which are discontinuous in time.

3.16). For wood deposition and all respiratory losses (except from leaves), the rate expression included the following temperature factor, $F(T)$, based on mean monthly air temperature (1955–70 average):

$$F(T) = 0.35 (40 - T) \exp [-(40 - T)/8] , \quad (9)$$

where T is temperature in °C. Thus the flow function in the temperature-dependent cases is of the form

$$\phi = KF(T)Q , \quad (10)$$

where Q is the value of the source compartment and K is a constant specific to that flow. The temperature factor initially was omitted from the leaf respiration function because mean air temperature varies only slightly during the growing season. However, data gathered this summer indicate the importance of even small temperature changes in leaf respiration rates and thus rates of net photosynthesis, particularly at low light intensities.

The gross photosynthesis function (GP) used in this model has the following form:

$$GP = (38.6 - 67.0 Q_1) \frac{Q_4(\text{final}) + 0.04}{0.07} Q_1 . \quad (11)$$

The first factor $(A - BQ)$ incorporates the postulate that, with increasing leaf biomass (Q_1), competition for light results in a decrease in GP per gram of leaves. The GP function also includes the final value of the bud compartment (Q_4) at the end of the dormant season (Fig. 3.16). Thus, the number of buds set during the previous growing season and surviving dormancy determines the number of leaves and therefore GP throughout the current season in this version of the model. Without this factor, the effect of conditions of the previous growing season was underestimated. Proposed work on the magnitude of vernal carbohydrate flux will improve this section of the model.

Model output is shown for a 20-year period as a graph of compartment values (dry weight organic matter per m²) vs time (Fig. 3.17). With the choice of values for model parameters shown in Fig. 3.16, the leaf biomass development curve agrees with measured values (see Fig. 3.2). At the same time, total gross photosynthesis, leaf and stem respiration, and annual woody growth agree with budget synthesis (Table 3.7). The model predicted that wood deposition begins after April 1 and continues into the fall. Likewise, the model predicted a leveling off of all metabolically active tissues after 20 years while woody tissue continued to increase.

Fig. 3.17. Time behavior of the compartments of the primary producer model. All compartment values are dry weights of organic matter per m^2 . The time scale is divided into two parts: 0 to 5 years and 16 to 20 years.

As experimental results become available, this model will be updated accordingly. For example, based on gas exchange and light extinction measurements initiated this year, functions for GP which include light intensity and soil moisture will need to be derived. The inclusion of a temperature and bud biomass factor in leaf respiration and replacement of instantaneous litter-fall by measured leaf retention curves will be completed. Eventually woody tissue will be compartmentalized into four components -- branch, bole, tap root,

and large lateral roots -- with equations derived to describe the allocation of photosynthate to each. As stand growth data are analyzed for a range of site conditions, patterns of soil moisture and mineral status will be incorporated as driving functions. To meet objectives of our primary production program, other functionally important forest strata must be considered in order to evaluate productivity under natural and manipulated conditions. As a step toward attaining these objectives, this model has proven invaluable in

Table 3.7. Comparison of budget results with predictions from the primary producer model for 1970^a

All values are in kilograms per square meter per year (dry weight of organic matter)

	Leaf respiration	Tree respiration	Gross production	Tree growth
Budget results	0.42	1.19	2.37	0.29
Model prediction	0.39	1.21	2.29	0.28

^aBudget results are based on respiration data of Botkin et al. [D. B. Botkin, C. M. Woodwell, and N. Tempei, *Ecology* 51, 1057-60 (1970)]; tree growth is computed from diameter changes using allometric equations (Table 3.4); and gross production is computed by summing respiration, tree growth, litterfall, fine root death and respiration ($0.24 \text{ kg m}^{-2} \text{ year}^{-1}$), and insect consumption ($0.020 \text{ kg m}^{-2} \text{ year}^{-1}$).

defining directions for research and as a link to all other ecosystem processes which are dependent on accumulation of organic carbon and minerals.

SECONDARY PRODUCTION

R. I. Van Hook

G. J. Dodson	M. G. Nielsen
R. Gaskins	D. E. Reichle
R. A. Goldstein	M. H. Shanks
J. F. McBrayer	P. Sollins

Secondary production encompasses those organisms not responsible for photosynthesis or chemosynthesis but which utilize net primary plant production. There are three components included in the study of secondary producers which include (1) the effects of secondary production on primary producers of the forest ecosystem, (2) secondary production important to man's needs (both as food sources and as competitors for resources), and (3) the functional role of animals in ecosystem processes (energy flow and nutrient cycling) which contribute to basic ecosystem integrity. Evaluation of secondary producers with the forest ecosystem from the standpoint of these three major components requires fairly detailed process research designed to provide reliable estimates of mineral turnover, energy flow, population dynamics, and food preferences and feeding habits. Mechanistic models describing certain aspects of secondary production may then be derived which relate the information obtained on these parameters to the total ecosystem process.

Population Dynamics of a *Liriodendron* Canopy Aphid Population

Biomass and density of the *Liriodendron* canopy aphid population (*Macrosiphum liriodendroni*) were determined for the 1971 growing season. The sample data were collected from three trees accessible from a 29-m tower and included aphid numbers subdivided into one of six life stages (four immature instars, subalats, and alats), canopy location, and gross leaf area at each sample position. Biomass was expressed as milligrams of dry weight of aphid per square meter of leaf surface for the different canopy levels and 6 life stages at 19 sampling periods.

Population data were sorted and analyzed with Pitfall-1¹⁹ for temporal differences and for differences due to life stage or canopy location. Aphid biomass varied seasonally as shown in Fig. 3.18. Aphids appeared in late April, approximately one week after leaf emergence. Population biomass increased up into mid-May, at which time maximum population biomass occurred (about 38 mg/m^2 of leaf surface). Aphid biomass then declined rapidly until late June, after which time the biomass decline proceeded at a less rapid rate into late August in response to adverse environmental conditions and a significant reduction in the flow of minerals, carbohydrates, and lipids from roots to leaves. As environmental conditions of temperature and humidity improved and as nutrient resources began to move from leaves back into the tree, the aphid population biomass increased to a second much smaller peak of 3 mg/m^2 of leaf surface at the end of September. The aphid population biomass then decreased to zero by mid-October, approximately one month before all leaves had fallen.

Further analyses of aphid population biomass data demonstrated significant differences ($P \leq 0.05$) between two groupings of life stages: immature instars I-IV and a subalate-alate grouping. There were also significant differences ($P \leq 0.05$) between biomass estimates at the three canopy levels. Therefore, further utilization of this information as a data base for developing models of energy flow and nutrient fluxes through the aphid population will necessitate consideration of individual life stage groupings and canopy levels as well as the temporal variations shown in Fig. 3.18.

19. N. C. Hull, J. J. Beauchamp, and D. E. Reichle, "Pitfall-1," ORNL-IBP-70-2 (1970).

Fig. 3.18. Mean *Liriodendron* canopy aphid population biomass for all life stages of *Macrosiphum lirioidendroni* during the 1971 growing season. Values represent combined means of 50 samples from three canopy levels (level 1 = 21 to 23 m, level 2 = 17 to 21 m, and level 3 = 12 to 17 m). Error bars represent $\pm$ one standard deviation. Biomass was determined after 24 hr of drying at 70°C.

Dynamic Model of Canopy Insect Grazing

Utilizing leaf growth and "apparent" leaf consumption data (observed leaf hole area) for the 1967 growing season from a yellow poplar (*Liriodendron tulipifera*) stand in eastern Tennessee, a canopy grazing model was developed and implemented to determine insect consumption as a function of leaf generation and time. The mean consumption rate expressed as a function of leaf generation and time is given by

$$\bar{c}_j(t) = \frac{dH_j(t)}{dt} + \frac{dG_j(t)}{dt} \cdot \frac{1}{G_j(t)} \cdot H_j(t), \quad (12)$$

where $\bar{c}_j(t)$ = the mean consumption rate for generation j at time t , $H_j(t)$ = mean leaf hole area for generation j at time t , and $G_j(t)$ = mean gross leaf area for generation j at time t .

To obtain continuous estimates of gross leaf area and leaf hole area, field measurements were fitted to the nonlinear function

$$y = \alpha + (\beta - \alpha)e^{-\lambda t}$$

with $y = G_j$ or H_j , α = maximum observed area, β = minimum observed area, and λ = growth rate parameter.

Results of these analyses are shown in Figs. 3.19 and 3.20 for gross leaf areas and leaf hole areas, respectively. Error bars represent $\pm$ one standard error of the mean. As illustrated in both figures, growth of leaves and holes reaches an asymptotic maximum in generations one, two, and three during the growing season. However, neither gross leaf area nor leaf hole area reach an asymptotic maximum in generations four and five, but continued to increase to the end of the growing season.

Net leaf area was then determined for each leaf generation through time from

$$N_j(t) = G_j(t) - H_j(t). \quad (13)$$

These estimates were then utilized in determining cumulative percent consumption for each generation from

$$X_j(t) = \frac{\int_0^t \bar{c}_j(t) dt \cdot 100}{N_j(t) + \int_0^t \bar{c}_j(t) dt} \quad (14)$$

Fig. 3.19. Mean gross area (cm^2) for five generations of *Liriodendron* leaves expressed as a function of time. Error bars represent one standard error of the mean. Solid lines through the data points represent the best nonlinear least-squares fit.

Total canopy consumption through time was then estimated from

$$Y(t) = \frac{\sum \nu_j \bar{N}_j X_j}{\sum \nu_j \bar{N}_j}, \quad (15)$$

where ν_j = the ratio of the number of leaves from a sample in generation j to the total number of leaves and $\bar{N}_j$ = the mean net leaf area of generation j at time t . The results of these calculations are shown in Table 3.8. These values represent absolute percent consumption during the growing season. Second-generation leaves were most heavily fed upon for the entire season, although fourth-generation leaves were consumed to a greater extent during the early weeks. Total insect consumption of canopy foliage was estimated to be 2.51% of the available leaf area. This estimate provided by the canopy grazing model was 34.5% of the estimate derived from the September 20 data of gross leaf area (Fig. 3.19) and observed hole area (Fig. 3.20) which

was 7.28% of available leaf area. This means that estimation of insect consumption by single end-of-the-season observations resulted in an estimate of three times the actual value. It should be pointed out, however, that 2.51% insect consumption resulted in a 7.28% loss of photosynthetic surface by September 20. Therefore, of an annual leaf production by *Liriodendron* of 249 g/m^2 , 2.51% or 6.3 g/m^2 was consumed by insects, which resulted in a 7.28% or 18.1 g/m^2 loss of photosynthetic surface. These results suggest that previous estimates of insect consumption in various forest stands be reexamined taking into consideration particular patterns of canopy foliage development in evaluations of the significance of canopy grazers.

Energy Dynamics of Spider-Prey Populations

Spiders are the dominant invertebrate predator within the *Liriodendron* forest litter population in terms of

Fig. 3.20. Mean area (cm^2) of holes found in five generations of *Liriodendron* leaves expressed as a function of time. Error bars represent one standard error of the mean. Solid lines through data points represent the best nonlinear least-squares fit.

Table 3.8. Estimated percent canopy consumption (cm^2 leaf eaten per 100 cm^2 of leaf area) for five leaf generations and for the entire canopy during the 24-week growing season

Weeks	Mean cumulative percent leaf consumption					Total canopy
	Gen-1	Gen-2	Gen-3	Gen-4	Gen-5	
1	0.00	0.03	0.51	1.82	0.32	0.27
2	0.00	0.23	0.69	2.03	0.42	0.38
3	0.05	0.46	0.86	2.04	0.47	0.51
4	0.16	0.70	1.02	2.00	0.51	0.67
5	0.28	0.94	1.19	1.97	0.55	0.82
6	0.40	1.19	1.35	1.95	0.59	0.98
7	0.53	1.42	1.50	1.93	0.63	1.13
8	0.65	1.65	1.65	1.92	0.68	1.28
9	0.76	1.87	1.79	1.92	0.73	1.42
10	0.86	2.08	1.92	1.92	0.77	1.55
11	0.96	2.28	2.04	1.93	0.82	1.67
12	1.05	2.47	2.15	1.94	0.88	1.78
13	1.13	2.64	2.25	1.95	0.93	1.88
14	1.20	2.80	2.33	1.96	0.99	1.97
15	1.26	2.94	2.41	1.98	1.04	2.06
16	1.32	3.07	2.48	2.00	1.10	2.13
17	1.37	3.19	2.55	2.01	1.16	2.20
18	1.41	3.30	2.60	2.03	1.22	2.26
19	1.45	3.40	2.65	2.05	1.28	2.32
20	1.48	3.49	2.69	2.06	1.34	2.36
21	1.51	3.57	2.73	2.08	1.40	2.41
22	1.54	3.64	2.76	2.10	1.46	2.44
23	1.56	3.70	2.79	2.11	1.52	2.48
24	1.58	3.76	2.82	2.13	1.59	2.51

numbers and biomass. Mean annual population density ($126 \text{ individuals/m}^2$) exceeded the collective population density of the next two most numerous predator groups, Chilopoda and predaceous Coleoptera, by approximately 1.3 times. Mean spider biomass (42.7 mg/m^2) was nearly 1.3 times that of chilopods and 1.4 times that of predatory beetles. The impact of spiders on community dynamics, however, can best be interpreted through their contribution to energy flow through the invertebrate community.

Ingestion, assimilation, and respiration rates were derived for the three spider classes ($<0.1 \text{ mg}$, $1 \text{ to } 10 \text{ mg}$, and $>10 \text{ mg}$ dry body weight). Ingestion (mg of food per individual per day) was calculated from

$$I = \frac{\lambda Q_e}{P\alpha Q_f} \quad (16)$$

utilizing field ^{13}C equilibrium values for spiders (Q_e) and prey (Q_f) and laboratory measurements: ^{13}C elimination rates (λ) and isotope assimilation fractions

(P and α). Mean annual Q_e and Q_f for each size class were used in calculating consumption. Q_{10} temperature corrections for λ were included in these calculations. Assimilation by spiders was estimated from direct laboratory measurements of weight of prey ingested relative to weight of feces egested (ingestion - feces = assimilation). Respiration rates and their temperature adjustments were determined from

$$\log \mu\text{l O}_2 \text{ g}^{-1} \text{ hr}^{-1} = 3.3 - 0.4 \log (\text{body size}) \quad (17)$$

Calorific equivalents of food ingested and assimilated at various temperatures were related to O_2 respired by assuming an R.Q. = 0.8 ($\mu\text{l O}_2 = 0.0048 \text{ cal}$).

Interpretation of these results reveals that spiders operated at positive energy balance only within a fairly narrow temperature range (Fig. 3.21). Below 5°C spiders became sluggish and ceased feeding. Assimilated energy approached respiratory energy losses at approximately 5°C ; below this temperature, spiders must utilize stored energy to meet metabolic needs. Spiders in the litter stratum do not undergo true diapause but enter a state of torpor during periods of lower temperature in winter. Activity and feeding are resumed during warm days throughout the winter. From 5 to 20.5°C , small spiders assimilate more energy than is respired, with an optimum net balance occurring between 10 and 15°C . Energy not utilized in respiration can be channeled into growth and reproduction. Above 20.5°C , the respiratory rate accelerates sharply, while above 25°C the ability to maintain a positive energy balance declines rapidly. Spiders respond to high-temperature stress by seeking cooler habitats or by aestivating during unfavorable environmental conditions. Net weight change was zero for medium-sized spiders at 5 and 18°C , with growth and reproduction possible over a temperature range of only 13°C . Respiration of large spiders also exceeded energy assimilation at approximately 18°C .

Mean monthly temperatures measured at the air-litter interface in the *Liriodendron* forest average 13.3°C for the year, which is within the optimal temperature range (10 to 15°C) for spiders in all three size classes. Spiders could remain active for substantial periods during all months except February ($\bar{X} = 2.4^\circ\text{C}$), June ($\bar{X} = 22.3^\circ\text{C}$), and August ($\bar{X} = 21^\circ\text{C}$). Temperature extremes occasionally were encountered which would force spiders into temporary periods of inactivity. Spiders were not entirely inactive during such periods, but probably foraged during the warmer daylight hours in mid-winter and during the cooler nighttime hours throughout the summer. Hunting and feeding during

Fig. 3.21. Relationship of changes in metabolic rates, ingestion rates, and assimilation rates (cal/individual/day) correlated with temperature for (a) small, (b) medium-sized, and (c) large spiders.

the hot summer were possible at night when temperatures moderated, explaining an adaptive value of nocturnal habits of these species.

Bioenergetic Model of Earthworms

In ecosystems of temperate regions, earthworms are one of the major decomposer organisms responsible for litter fragmentation and mixing of organic components with mineral soil. Suppression of earthworm populations with pesticides has often resulted in marked reduction in site fertility, and introduction of these species has been recommended as a means of improving the mineral status of ecosystems on poor soils. Thus earthworms are an important component in assuring the integrity of the system.

The bioenergetic relationships of the decomposer complex of the *Liriodendron* forest floor were utilized in developing a "carbon model" of litter breakdown, which describes the rate of organic detritus mixing into mineral soil due to the activities of the earthworm population. From biomass data on the O_1 and O_2 litter compartments, soil organic matter, and the earthworm population, and from data on ingestion and metabolism of earthworms, the "carbon model" was evaluated for this subsystem.

The model (Fig. 3.22) consists of a set of seven simultaneous, nonlinear differential equations, plus several time-dependent forcing functions, which were solved using a fourth-order Runge-Kutta method with a step size of 0.1 month. Transfer from the O_1 compartment to O_2 and from O_2 to soil as well as respiratory losses from all compartments were assumed to be linear functions of the source compartment. Root death input to the soil was considered a constant $100 \text{ g m}^{-2} \text{ yr}^{-1}$; litterfall was treated as an instantaneous event occurring on October 1.

Additional assumptions involving dynamics of the earthworm compartment were:

Compartments

$X_1 = O_1$ litter horizon with initial conditions of 200 g/m^2 ,

$X_2 = O_2$ litter horizon with initial conditions of 260 g/m^2 ,

X_3 = total earthworm biomass with initial conditions of 14 g/m^2 ,

X_4 = total soil organic matter to depth of 35 cm; initial conditions of $1.3 \times 10^4 \text{ g/m}^2$,

X_3' = extractable earthworm biomass estimated from X_3 using a soil temperature and moisture function.

Transfer functions

r_3 = earthworm respiration in equivalents of organic matter ($\text{g m}^{-2} \text{ year}^{-1}$), R_3 = body size respiration estimate, $K_T = aQ_{10}$

$= R_3(365)K_T X_3$, where $R_3 = 10.8 \text{ mg g}^{-1} \text{ day}^{-1}$ at 20°C .

$f_{2,3}$ = ingestion of O_2 litter by earthworms ($\text{g m}^{-2} \text{ year}^{-1}$), calculated from ^{137}Cs input-loss equations describing mass balance of isotope in soil organic matter and earthworm tissue

$= 0.9/(365)X_3$, where $I, \text{g g}^{-1} \text{ day}^{-1}$, $= e^{0.1374(T-15)}$,

$f_{4,3}$ = ingestion of soil organic matter ($\text{g m}^{-2} \text{ year}^{-1}$), calculated same as $f_{2,3}$ except for 0.1 scaling factor,

$f_{3,4}$ = egestion plus mortality ($\text{g m}^{-2} \text{ year}^{-1}$)

$= (1 - p_2)(f_{2,3} + f_{4,3}) + BX_3$, where p_2 = assimilation ratio = 0.2, B (mortality) = 0.0052 day^{-1} .

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Fig. 3.22. Compartment model of litter decomposition and organic matter incorporation into soil, including the impact of soil-feeding earthworms on this process. Compartment and transfer symbols and their ecological interpretation are described in the text.

The model (Fig. 3.23) is remarkably stable when allowed to run for repeated years, even though there are considerable seasonal fluctuations in some compartments. Translated, this output provides the following information:

1. Ingestion of organic matter by earthworms amounts to $208 \text{ g m}^{-2} \text{ year}^{-1}$ at a rate varying between 3 and 50 g of detritus per g of earthworm per year.
2. Egestion amounts to some $167 \text{ g m}^{-2} \text{ year}^{-1}$ with $40 \text{ g m}^{-2} \text{ year}^{-1}$ of organic matter being assimilated by the earthworms.
3. Of the $40 \text{ g m}^{-2} \text{ year}^{-1}$ assimilated, 34.5 g are lost in respiration and 5.6 g are lost through mortality.

Although it is presently impossible for us to distinguish what proportion of the earthworm's diet is soil organic vs surface litter, the calculated ingestion rate is equivalent to turnover of approximately 75% of the mean annual standing crop of O_2 . With an average organic matter content of the A horizon at about 4.5%, earthworms would be processing $5 \text{ kg m}^{-2} \text{ year}^{-1}$ of soil. Assuming uniform distribution of the population

to 35 cm, this would be equivalent to a 70-year turnover time of soil due to earthworm feeding activities.

DECOMPOSITION PROCESSES

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The objective of the terrestrial decomposition research program is to provide data which will permit predictions about the dynamic behavior of the forest floor decomposer subsystem as a function of its state and driving variables. More specifically the objectives are to relate metabolic activity of the decomposer compartment with variables such as temperature, moisture, ATP content, microbial and invertebrate populations and trophic levels, and seasonal litter fall and standing crop patterns, and ultimately to correlate these data with rates of litter decomposition and subsequent mineral release. Experimental manipulations of decomposer compartments, such as by forest fertilization, are designed to elucidate the factors governing the state variables.

Seasonal Patterns of Litterfall and Standing Crop

Seasonal patterns of litterfall from representative species within a mesophytic forest stand dominated by yellow poplar (*Liriodendron tulipifera*) are shown in Fig. 3.24. Total annual litterfall, not including large branches and boles, was 331 g m^{-2} (Table 3.9). Leaves represented 83.3% of the total, reproductive parts 13.1%, and twigs 3.6%. Yellow poplar leaves made up 57% of the total leaf input, oak 12%, ash 8.8%, hickory 8.2%, red maple 1.6%, and miscellaneous species 12.6%, including predominantly understory species such as dogwood, redbud, and cherry.

Similarly, the litter horizons show seasonal patterns of litter standing crop for the O_1 and O_2 litter (Fig. 3.25), but distinct peaks in biomass do not occur because periods of input and most rapid decomposition are concomitant. Although 20 0.01 m^2 samples were collected at each point in time, seasonal patterns were not visible with respect to total litter. No increase in total standing crop is visible in the fall. Horizontal movement of litter due to wind and rain appears to be very important, and much more intensive sampling may be necessary before meaningful standing crop data can be obtained.

Fig. 3.23. Carbon flow through the earthworm component and the substrate of the decomposer subsystem in the *Liriodendron* forest.

Fig. 3.24. Seasonal patterns of litterfall for the major tree species in a *Liriodendron* forest ecosystem. Values given in $mg\ m^{-2}\ day^{-1}$, except for tulip poplar which are expressed in $g\ m^{-2}\ day^{-1}$, were calculated from mean total litterfall collected in a given number of days in 25 litter baskets located within a $20 \times 20\ m$ plot.

Table 3.9. Seasonal patterns of litterfall in a sinkhole area near the cesium-tagged *Liriodendron* forestLitter collected in 25 0.25-m² traps within a 20 × 20 m² plot. Amounts are in g dry weight per m².

Date	Yellow poplar	Ash spp.	Hickory spp.	Oak spp.	Red maple	Miscellaneous leaves	Twigs	Reproductive parts	Total leaves	Total
5/25/70*	0.35	0.35	0.19	0.47	0	3.98	2.47	12.57	5.45	20.49
9/29/70	5.90	0.85	0	0.50	0.02	6.08	1.77	1.90	13.36	16.33
10/5/70	49.61	6.68	6.21	0.56	0.16	8.35	0.49	1.75	71.57	73.32
10/12/70	43.06	5.82	5.41	0.50	0.14	7.27	0.66	0.10	62.41	63.17
10/21/70	10.47	1.19	0.98	0.46	0.09	1.06	0.08	0.19	14.26	14.52
10/27/70	17.52	4.22	3.09	1.41	0.17	1.47	0.02	0.49	27.87	28.39
10/30/70	10.61	3.36	2.52	1.20	0.63	1.22	0.28	0.29	19.53	20.10
11/2/70	7.40	0.68	2.61	7.45	0.57	2.01	0.44	1.30	21.13	22.86
11/5/70	2.20	0.21	0.48	1.21	0.26	0.15	0	2.53	4.46	6.98
11/25/70	4.34	0.52	0.56	12.58	1.69	1.67	0.16	10.31	21.36	31.82
12/10/70	0.80	0.21	0.22	2.33	0.03	0.24	0.02	5.35	3.83	9.21
1/25/71	1.25	0.20	0.07	0.16	0.04	0.46	1.53	2.66	2.17	6.36
3/22/71	3.06	0.04	0.20	3.89	0.31	0.86	4.94	4.05	8.34	17.33
Total	157.11	24.33	22.54	32.72	4.45	34.82	12.16	43.49	275.74	330.88

*Litter traps were first set out April 20, 1970.

Fig. 3.25. Seasonal changes in litter standing crop in the same *Liriodendron* stand in which litterfall was collected (see Fig. 3.24). Values represent means calculated from 25 0.01 m² samples taken each sampling period.

Forest Floor Respiration

Evaluation of CO₂ from the forest floor of a mesophytic *Liriodendron* forest is estimated to be ~3800 g m⁻² year⁻¹. The 3800 total is based on biweekly 24-hr measurements with an infrared gas analyzer (IRGA). Air was pulled through ten chambers inverted over the forest floor at a rate of 56 liters/hr. Flow rates of 25 to 275 liters/hr gave no significant differences in the amount of CO₂ evolved. IRGA values compared favorably with those obtained using KOH as the CO₂ absorber at low temperatures but not as favorably at higher temperatures; for example, KOH values were 90% of IRGA values in March but only 65% in June. Of the total of 3800 g, 2150 g is evolved from the soil and 1650 g from the litter. Annual total CO₂ evolved from small roots (<5 mm diam) is estimated to

be ~1390 g year⁻¹ m⁻² (or 65% of the CO₂ evolved from the soil). This value assumes a Q₁₀ of 2 and is based on biweekly measurements of daily mean soil temperatures, a mean value of 0.265 mg CO₂ evolved per hr per g of small roots (measured on a differential respirometer at 22°C), and an estimate of small root biomass of 0.5 kg/m². Of the 1650 g of CO₂ evolved from the litter 67% came from the O₁ horizon and 33% from the O₂ horizon. Annual total CO₂ evolved (3800 g/m²) from this forest floor is slightly higher than the 3400 g/m² estimated for the Brookhaven oak-pine forest from CO₂ measurements made during temperature inversions.²⁰

20. G. M. Woodwell and W. R. Dykeman, *Science* 154, 1031-34 (1966).

Annual gross production for the *Liriodendron* forest, estimated from photosynthesis measurements, is 4000 to 5000 g m⁻² year⁻¹. Of this total 1500 to 2400 g becomes incorporated into the soil and forest floor and is available for loss by respiration and mineral release. One g of CO₂ evolved is equivalent to 0.614 g of dry matter catabolized, assuming carbohydrate (C₆H₁₀O₅) is the substrate; then the annual loss of dry matter through respiration from this forest floor (including roots, soil organisms, and organic matter) is about 2300 g m⁻² year⁻¹.

We have considered only temperature and moisture as driving variables for mean daily changes in respiration rates. Age of litter no doubt influences seasonal changes in rates of respiration; that is, rates increase following leaf fall. However, this increased metabolism after leaf fall may also be related to the ideal temperature and moisture conditions that usually exist for the decomposer compartment during the fall season.

Rates of respiration determined in the laboratory by O₂ consumption measured with a differential respirometer were about one-third as high as the field

measurements (Fig. 3.26). These lower measurements may be due to the short duration of the laboratory measurements, the inability to duplicate temperature and moisture changes which occur in the field, and the otherwise static conditions under which measurements were taken. Fig. 3.27 illustrates the importance of the 24-hr measurement period in the field; that is, even though litter temperature and moisture changed very little during the 24-hr period, the CO₂ evolved ranged from 125 to 594 CO₂ mg m⁻² hr⁻¹. This indicates that during a given 24-hr period factors other than temperature and moisture are influential in determining the rate of respiration. One possible controlling variable during this particular 24-hr period was vapor pressure deficit also shown in Fig. 3.27. Carbon dioxide may be absorbed more readily into air which is saturated with moisture, thus causing an increased rate of diffusion from the soil and litter into the atmosphere. Other variables which may have a role in controlling respiration rates are diurnal activities of certain soil organisms and available oxygen.

The synergistic effects of moisture and temperature on respiration rates are most evident at microclimatic extremes (Fig. 3.26). For example, at temperatures below 10°C respiration rate is influenced very little by moisture conditions (Fig. 3.28); moisture becomes more limiting as temperatures reach the optimum.

Microbial Decomposition Processes

Relating metabolic activity of soil and litter microorganisms to their population sizes and/or biomass is a problem being approached through the use of standard techniques (plate counts for bacteria and fungi) and newer techniques such as by ATP analysis and comparing these to gas exchange measurements. Microbial populations, determined by plate counts at biweekly intervals through one year, varied with changes in temperature and moisture. Low counts of bacteria in both litter layers and soil occurred in August when conditions were quite dry. High bacterial counts from O₁ horizons occurred in September, from O₂ horizons in June, and from soil in April. Any biotic effects on microfloral populations were overshadowed by moisture and temperature effects. One possible exception was a high count of bacteria in O₁ litter in late September when leaf fall began. This high count could be accounted for by a rapid colonization by bacteria of freshly fallen leaves. However, moisture and temperature conditions were also ideal during this time. Moisture seems to have a greater effect than temperature on bacterial and fungal populations (Fig. 3.29) at

Fig. 3.26. Comparison of O₁ litter respiration rates determined in a differential respirometer with in situ rates measured with an infrared gas analyzer and correlations of these measurements with temperature and moisture. In situ measurements were converted from CO₂ to O₂ using an RQ value of 0.85. R = 0.64 for IRGA data and 0.83 for respirometer data.

Fig. 3.27. Diurnal cycle of CO₂ evolution from the *Liriodendron* forest floor in early May 1971. An inverse correlation with vapor pressure deficit (calculated from air temperature and relative humidity data) is shown. Litter moisture = 45% of dry weight; soil moisture = 24%.

Fig. 3.28. Comparison of oxygen uptake by O₁ litter as a function of moisture content at three different temperature ranges. Curves fitted by eye.

temperatures above 10°C. Temperature becomes the limiting factor at and below about 10°C even though moisture conditions may be ideal. This same trend is

observed in respiration rates (Fig. 3.27). Annual population means and ranges with accompanying moisture, temperature, and respiration data are given in Table 3.10. Fungal and bacterial populations are higher in the O₂ horizon than in soil or the O₁ horizon, while respiration rates per gram of substrate are higher in the O₁ horizon. High respiration rates in the O₁ horizon as determined by oxygen uptake measurements in a differential respirometer agree with CO₂ evolution data as measured by infrared gas analysis in the field. Respiration rates are much more variable in the O₁ horizon than in O₂ litter and soil (Table 3.10), as is moisture and temperature.

Significant differences in rates of dark O₂ consumption as compared with those measured in the light suggested the presence of photosynthetic organisms in the litter and upper soil horizon. Subsequent extraction of substrate with acetone yielded an average of 0.116 mg of chlorophyll per gram of litter and 2.94 µg per gram of soil. Assuming 5 mg chlorophyll per gram dry

Table 3.10. Annual means and ranges of litter and soil temperatures, moisture, respiration rates, and microfloral populations in *Liriodendron* forest calculated from biweekly samplings through one year

Respiration rates determined with a differential respirometer at field moisture and temperature.
Microfloral counts are per gram of dry weight of substrate.

Compartment	Temperature (°C)		Moisture (% of dry wt)		Respiration rate ($\mu\text{l O}_2 \text{ g}^{-1}$ substrate)		Bacteria ($\times 10^{-6}$)				Fungi ($\times 10^{-6}$) plate counts	
	Mean	Annual range	Mean	Annual range	Mean	Annual range	Plate counts		Direct counts		Mean	Range
							Mean	Range	Mean	Range		
O ₁ litter	15.8	2-24	104	14-262	123	0-443	0.2275	0005.5-0919.9	1907.8	0686.7-5060.0	0002.7	0000.25-0006.8
O ₂ litter			134	32-280	75	7-189	0.2485	0008.8-1835.0	2287.8	0603.8-6940.0	0124.2	0000.41-0475.4
A ₁ soil to 5 cm			44	19-117	6	2-12	0.0056	0000.8-0047.0	1211.9	0275.9-6100.0	0000.3	0.0-0003.2

Fig. 3.29. Seasonal trends of bacterial and fungal populations (plate counts), respiration rates, moisture, and temperature in the O_2 litter of the *Liriodendron* forest plot.

weight of algae,²¹ this would represent 23.2 mg dry wt of algae per gram of litter and 0.5 mg of algae per gram of A_1 soil. Measurements were made with a Beckman spectrophotometer at a wavelength of 663 m μ . The absorption spectrum (Fig. 3.30) showed a peak for chlorophyll *a* only. This is characteristic of algae other than the green algae. It is possible that much of the pigment extracted came from blue-green algae, and if so they should be given consideration as possible nitrogen fixers in this system.

Direct counts of bacteria, using a Howard Mold counting chamber, were much higher than plate counts (Table 3.10), since dead and dormant cells were counted by the direct but not by the plate count method. Plate counts select for those microorganisms which will grow on the substrate being used. Direct counts agree with plate counts in that the higher counts occurred in the O_1 litter and the lower counts occurred in the soil.

Seven methods of ATP extraction have been compared for the purpose of finding the most efficient technique for extracting ATP from soil and litter microorganisms for biomass estimates. Laboratory microcosms consisting of kaolinite, sand-kaolinite, and

21. F. E. Round, p. 159 in *The Biology of the Algae*, Edward Arnold Ltd., London, 1965.

sand were used as substrates. Three levels of disodium salt of ATP (1.0, 0.5, and 0.1 $\mu\text{g/g}$) were added to the microcosms. Results of subsequent ATP assays are given in Table 3.11. ATP was consistently least efficiently extracted from clay; butanol and sulfuric acid methods were most efficient in all substrates, but were in no case significantly different from each other. The ATP assay is accomplished exploiting the light-emitting reaction of ATP with luciferin of the firefly (*Photinus pyralis*) enzyme system. Light is quantitatively measured using the ORNL Analytical Chemistry Division's adapted GeMSAEC system. A lighttight box and parallel mixing disk circumvent problems encountered in liquid scintillation assay, that is, the necessity of premixing reagent and sample solutions. Samples are compared with internal standards by a program contained in the accompanying PDP-8 computer. ATP values of samples and standards are summarized and graphed as computer

Table 3.11. Extraction efficiencies ($\pm\text{SE}$) of several methods for ATP removal from three substrates in microcosms

Method of extraction	Substrate	Average efficiency
Tris	clay	44.2 $\pm$ 3.3
	sand-clay	67.6 $\pm$ 3.4
	sand	73.7 $\pm$ 3.1
N-bromosuccinimide	clay	40.5 $\pm$ 6.7
	sand-clay	63.6 $\pm$ 3.3
	sand	61.2 $\pm$ 11.1
Butanol	clay	86.6 $\pm$ 4.1
	sand-clay	89.8 $\pm$ 1.9
	sand	95.8 $\pm$ 1.8
DMSO, acid	clay	37.0 $\pm$ 5.7
	sand-clay	64.5 $\pm$ 2.9
	sand	79.5 $\pm$ 5.1
DMSO, neutral	clay	50.3 $\pm$ 12.6
	sand-clay	87.2 $\pm$ 2.9
	sand	88.9 $\pm$ 3.2
Sulfuric acid	clay	86.8 $\pm$ 6.4
	sand-clay	85.3 $\pm$ 3.6
	sand	98.7 $\pm$ 0.2
Perchloric acid	clay	44.9 $\pm$ 4.4
	sand-clay	83.1 $\pm$ 7.9
	sand	91.4 $\pm$ 2.7

Fig. 3.30. Absorption spectra of chlorophyll extracts from litter and soil collected in the *Liriodendron* forest in July 1970.

printout. Absolute values obtained using the GeMSAEC system are being validated using ^{32}P -tagged ATP.

ATP assay provides a rapid and accurate estimation of metabolically active microbial biomass. Estimates of a known titer of *Bacillus subtilis* in logarithmic growth phase were made using direct observation, dilution plating, and ATP assay (Table 3.12). Assuming 3.9×10^{-9} μg of ATP per bacterial cell,²² the ATP assay estimated the known titer with greater precision and accuracy than the other methods.

Energy Dynamics and Trophic Structure

Food chains are the biotic pathways of energy and nutrients in ecosystems, that is, the routes of transport and exchange of materials among components. Organisms have evolved the ability to transform chemical energy of organic matter, thereby deriving sustenance and contributing to increasing entropy of the system. Consequently, analyses of ecosystems generally utilize a bioenergetic basis for evaluating processes.

22. G. V. Levin, C. S. Chen, and G. Davis, Aerospace Medical Research Laboratory, Tr-67-71 (1967).

Table 3.12. Estimation of a known titer of bacteria (*Bacillus subtilis*) in logarithmic growth phase in a silt-loam microcosm

Known titer	Method of estimation	Estimates of titer $\bar{x}$ of replications ^a					
		1	2	3	4	$\bar{x}$	SE
2.1×10^9 cells/g	Direct observation	4.7×10^8	0.16×10^8	0.49×10^8	0.092×10^8	1.3×10^8	0.96×10^8
	Soil dilution plate	2.6×10^7	0.49×10^7	0.98×10^7	67.0×10^7	17.7×10^7	14.2×10^7
	ATP analysis	1.0×10^9	0.9×10^9	1.8×10^9	1.4×10^9	1.27×10^9	0.17×10^9

^aEach replication is composed of four samples.

The diversity of food habits in the decomposer community is exceedingly complex, with a variety of potential food bases all originally derived from the input of detritus. The litter horizons of forest soil show consistent energy contents when the values are corrected for discrepancies in ash content due to mixing with mineral soil (Table 3.13). When expressed as calories per gram of ash-free dry weight, surface leaf litter (including associate microbial populations) averages 4870 ± 11 cal/g. Woody materials, including both surface litter and roots, average 5127 ± 125 cal/g ash-free dry weight. During humification and incorporation of these organic materials within the mineral soil, there is a decrease in their chemical energy content. Particulate soil organic matter averages 2758 ± 309 cal/g ash-free dry weight, with a progressive reduction in caloric value with greater depth in the soil horizon.

The activities of soil invertebrates accomplish soil turnover and aeration and, through symbiosis with microbial populations, the eventual release and recycling of nutrients in the ecosystem.²³ The conceptual model of forest litter decomposition which has evolved is one in which larger invertebrates prepare suitable microbial substrates by grinding, wetting, or otherwise altering the physical properties of the litter. Smaller invertebrates then act as population regulators on the microflora. The product is then one of accelerated litter disappearance with slowed, stabilized nutrient element release.

Leaf litter is highly resistant to the digestive enzymes of most metazoa. Consequently, the larger invertebrates may lack essential nutrients in exploiting leaf litter. Table 3.14 presents evidence, from an experiment with

Table 3.13. Calorific contents of potential food sources for decomposer invertebrates of forest litter and soil horizons.

All values, except for woody materials, are from a mesic woodland dominated by *Liriodendron* and with a mul-type humus (October sampling).

Type of organic material	cal/g ash-free dry weight
Litter (leaves and small twigs)	
O ₁ horizon	4859
O ₂ horizon	4881
Particulate soil organic matter	
0-10 cm depth	3318
10-20 cm depth	2704
20-30 cm depth	2251
Woody materials	
Large roots	4880
Small roots	5290
Bark	5210
Fungal mycelia	4808

litter-grazing millipedes, in which microbial decomposition was both augmented and exploited, analogous to the rumen of grazing mammals but accomplished through coprophagy. Wetting and increasing pH favor a shift in microbial populations from fungi to bacteria, which are more effective decomposers. Bacterial decay is essentially a surface phenomenon, and gut passage greatly increased surface area. Caloric content, however, did not change significantly. Microbial activity thus increased the availability of energy and nutrients, the caloric utilization by the millipedes shown in Table 3.15. Work continues toward elucidating further symbiotic relationships between decomposer invertebrates and microflora.

Our predictive capability for estimating energy intake for the entire range of decomposer animals occurring in forest litter and soil is shown in Fig. 3.31. The energy

23. C. A. Edwards, D. F. Reichle, and D. A. Crossley, Jr., pp. 145-72 in *Analysis of Temperate Forest Ecosystems*, Springer-Verlag, Berlin-Heidelberg-New York, 1970.

Table 3.14. Effect of gut passage by *Apheloria montana* on some physical, chemical, and biological properties of litter

	Particle size (mm ²)	pH	Moisture (% dry wt)	cal/mg (dry wt)	Fungi ^a ($\times 10^4$)	Bacteria ^a ($\times 10^6$)
Litter	0.24	5.5	49.6	3.88	49 $\pm$ 5	76 $\pm$ 10
Feces	0.04	7.7	392.0	3.45	1 $\pm$ 0.2	116 $\pm$ 6

^aColonies per gram of dry weight coded as a negative power of 10; for example, fungal colonies per gram of dry weight litter equals 490,000.

Table 3.15. Differential energy budgets for the millipede *Apheloria montana* resulting from the presence or absence of feces in the diet (cal g⁻¹ day⁻¹ at 21°C)

	Litter plus feces	Litter only
Litter ingestion	111.3	256.7
Feces ingestion	105.5	
Total ingestion	216.8	256.7
Production	3.8	1.1
Respiration	13.8	12.2
Total assimilation	17.6	13.3
Primary egestion	105.5	243.4
Net egestion	93.7	243.4

balance of invertebrates is expressed as a logarithmic function of energy ingested to maintain this energy pool. The basic tenant of this model is that a given energy intake is required to maintain the integrity of a certain amount of potential energy in biomass. Calories consumed per individual per day are significantly correlated ($\alpha = 0.001$) across this broad range of organisms representing several trophic levels. A least-squares linear regression equation of the form

$$Y = aX^b \text{ (or } \log Y = \log a + b \log X \text{)}, \quad (18)$$

where $Y = \text{cal/day}$ and $X = \text{cal/individual}$, yields the following values: $a = 0.071$ and $b = 0.725$. Thus energy

Fig. 3.31. The energy balance of detritus-feeding invertebrates and their predators is expressed as a logarithmic function of food energy ingested necessary to maintain the organism's energy pool.

intake closely follows the body surface/volume relationship for food intake ($b = 0.67$) first postulated by van der Drift.²⁴ (Deviations from the regression model may be attributed to differences in the efficiency of energy assimilation.)

A second attribute exceedingly important to the energy balance of the ecosystem is the respiratory heat loss. Respiration rates are commonly measured as units of oxygen utilized, directly convertible to calories using the caloric equivalents of 0.0049 to 0.005 cal/ μ l O_2 . A general relationship exists between body size and metabolic rate for specific groups of organisms, but seldom has this relation been applied to decomposer invertebrates.²⁵ The correlation between maintenance metabolism (μ l O_2 /hr) and body size for decomposer invertebrates from all trophic levels is shown in Fig. 3.32. Single point measures for a great variety of different invertebrate groups were included (107 values from 4 phyla: Nematoda, Mollusca, Annelida, and Arthropoda), with each value representing a distinct taxonomic subgrouping. A least-squares linear regression ($\alpha = 0.0001$) of the form $Y = aX^b$, where $Y = \mu$ l O_2 /hr and $X =$ mg live body weight, yields the following values: $a = 0.339$ and $b = 0.808$. Respiration clearly follows a function approximating the surface/volume relationship, long recognized for vertebrates but only recently applied to invertebrates. Although minor deviations from the model may occur due to the influence on respiration of age, sex, season, and diurnal periodism, the predictive capability for average metabolic rates over a great range of size classes and food habits is excellent.

Organic Matter Decomposition Model

The decomposition model (Fig. 3.33) has been revised to reflect new data gathered or located this year and to take into account effects of temperature and moisture on decomposition rates. The arrangement of compartments and transfers is the same, although most of the input values and rate constants have been changed. Litterfall is still considered an instantaneous event, although the data are now available to describe the actual pattern over time by species. Root death is still assumed to be $100 \text{ g m}^{-2} \text{ year}^{-1}$ distributed uniformly throughout the year. However, recently gathered data suggest that this value may be too low by, perhaps, a factor of 2.

Each of the remaining transfers has been made an explicit function of mean monthly air temperature

(1955–70 average) and a relative monthly index of soil moisture status:

$$\phi = KM 2.45 (40 - T) \exp [(-40 - T)/8] Q, \quad (19)$$

Fig. 3.32. The correlation between maintenance metabolism (μ l $O_2 \text{ hr}^{-1}$) of decomposer invertebrates from all trophic levels and body size.

Fig. 3.33. Arrangement of compartments and flows in the decomposition model. Initial conditions (g/m^2 dry weight) are shown in boxes. Rate constants (year^{-1}) are shown next to the flows.

24. J. van der Drift, *Tijdschr. Entl.* (94), 1–168 (1950).

25. D. E. Reichle, *Ecology* 50(6), 1102–1104 (1969).

Fig. 3.34. Time behavior of two components of decomposition model (O_1 of intermediate decay rate and O_2 , see Fig. 3.33).

where ϕ is the transfer rate ($\text{g m}^{-2} \text{ year}^{-1}$), M is the soil moisture index (0.100%), T is temperature ($^{\circ}\text{C}$), Q is the value of the source compartment (g/m^2), and K is a constant specific to each transfer (hr^{-1}).

Output from the model (Fig. 3.34) shows decreased decomposition rates during winter and summer due to low temperatures and lack of moisture, respectively. These curves fall in the same range as standing crop measurements (Fig. 3.25). Assuming an annual increase in soil organic matter of 100 g/m^2 , total CO_2 evolved during a year was predicted to be 640 g/m^2 exclusive of roots compared with 920 g/m^2 for soil, litter, and large roots extrapolated from field CO_2 measurements. The next round of model improvements should see incorporation of an empirically derived temperature-moisture function, the observed litterfall pattern by species groups, and a more realistic estimate of the organic matter input due to root death.

MINERAL CYCLING

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Primary production, secondary production, and decomposition processes are intimately affected by the movement of energy, water, and nutrients in an ecosystem. The mineral input to, conversion within, and output from each of these processes is one determining factor regulating process dynamics and the

resultant balance of an ecosystem. Mineral output influences water quality; therefore, mineral cycling is intimately tied to hydrologic processes and must interface with them. Mineral cycling research efforts at the Oak Ridge IBP site are designed to elucidate the flow of nutrients within terrestrial systems and quantify inputs to aquatic systems through an understanding of land-water interactions. The preliminary syntheses which follow represent progress to date on quantifying mineral pools and transfers within terrestrial systems.

A Study of the Water Budget and Mineral Input by Throughfall, Wetfall, Dryfall, and Stemflow in a *Liriodendron* Forest

A complete mineral inventory requires an accurate estimate of the amount of nutrient input (exclusive of litter) to the decomposer component. In an oak forest, 17.7% of the N, 37.4% P, 72.8% K, 41.9% Ca, 70.7% Mg, and 97.1% Na in litter plus throughfall was provided by throughfall.²⁶ A considerably smaller input of minerals probably occurs as a result of precipitation scavenging from the atmosphere and from direct fallout from the atmosphere during dry weather. The objectives of the following research have been: (1) to measure the input of nutrients (Ca, Na, Mg, N, P, K) and water to the forest floor of a *Liriodendron* stand by throughfall, dryfall (particulate matter), stemflow, and wetfall (incident precipitation), (2) to estimate evaporation of intercepted precipitation as a measure of the storage capacity of the forest canopy, and (3) to determine year to year variation in measured parameters and to relate parameters to variables of phenology, precipitation patterns, and foliage leaching.

Three Wong samplers below the forest canopy within a $20 \times 20 \text{ m}$ plot collect dryfall and throughfall (throughfall collectors are closed except during precipitation). A control sampler above the canopy collects dryfall and wetfall. Collection troughs around five trees (three tulip poplars: 14, 16, and 19 cm diam; one oak: 11 cm diam; and 1 dogwood: 6 cm diam) collect stemflow. Total amount of water collected is measured biweekly, and subsamples are taken for mineral analysis. All collection bottles are acid washed after each collection period and a preservative (1-2 dichloroethane) added to throughfall, wetfall, and stemflow collectors to prevent the growth of microorganisms which metabolize nutrient elements. One liter of 0.1 N HCL is added to each dryfall collector. Litter or frass

26. A. Carlisle, A. H. Brown, and E. J. White, *J. Ecol.* 54, 87-98 (1966).

which reaches the throughfall and dryfall bottles through large cone-shaped screens is filtered out of the subsamples before they are analyzed. Throughfall, stemflow, and wetfall samples are filtered through Whitman No. 42 filter paper to remove particulate matter, while dryfall samples are filtered through a stainless steel screen (0.8-mm mesh) which allows particulate matter to pass through. This procedure prevents the remeasurement of dryfall in the throughfall, stemflow, and wetfall.

Total annual input of K, Ca, Na, and Mg by throughfall, stemflow, wetfall, dryfall, and litterfall are given in Table 3.16. Wetfall values shown in a separate column are included in the throughfall and total to forest floor values, since traditional methods of measuring throughfall include input of elements by incident precipitation (wetfall). Dryfall values represent particulate matter input to the canopy, measured by the sampler above the canopy. Below-canopy dryfall values for all elements tested were higher than above-canopy values (in the case of K by a factor of 3). This difference was due to input to the below-canopy collectors of large amounts of insect frass, pollen, seeds, etc., which lost elements to the acid solution of the dryfall collection bottles. Since these sources (insect frass, etc.) of input reach the forest floor and are included as a part of the litter, the above-canopy values when added to other input sources give a more realistic estimate of total input to the forest floor than below-canopy values. Arrangement of the different sources of element input in order of their importance depends on the element in question, that is, for K: throughfall, litterfall, wetfall, dryfall, and stemflow; Ca: litterfall, throughfall, wetfall, dryfall, and stemflow;

Na: litterfall, wetfall, dryfall, throughfall, and stemflow. Litterfall accounted for the largest input of elements tested except for K of which 67% was found in throughfall. Stemflow collects at the base of the tree where it may have significant effects on physical and chemical properties of the soil.²⁷

Twenty-five throughfall collection bottles equipped with funnels (12 cm diam) randomly distributed over a 20 X 20 m plot located near the Wong sampler plot gave annual total values which were significantly higher than the total to forest floor values given in Table 3.16, that is, for K 2 times as high, Ca 1.6, Na 1.2, and Mg 2.2. These high values were probably due to several differences in methods used in collecting the throughfall, including (1) no preservatives used to prevent microbial activity, (2) the use of flat screens (as opposed to cone-shaped) inside the funnels allowing leaves to collect in funnels, and (3) less frequent sampling (monthly) allowing more time for leaching from leaves which collected in funnels.

Seasonal patterns of element input seem to follow the precipitation pattern (Fig. 3.35). However, input of K and Ca was highest in September when rainfall was relatively low. Input of Mg was also high during this period. This supports the theory that large amounts of elements are leached from leaves just before leaf fall. Intensity of rainfall is not reflected in these graphs except by the length of time between collections. For example, the high amount of wetfall and throughfall between May 7 and May 14, a relatively short collection period, indicates rather intense rainfall. For this same

27. P. L. Gersper and N. Holowsychnuk, *Soil Sci. Soc. Amer. Proc.* 34, 779-86 (1970).

Table 3.16. Total annual input of K, Ca, Na, and Mg by wetfall, throughfall, dryfall, stemflow, and litterfall to a *Liriodendron* forest floor.

Totals represent sums of biweekly measurements.

Element	(kg/ha)					
	Total incident precipitation (wetfall) ^a	Total to forest floor	Throughfall	Dryfall ^b	Stemflow	Litter ^c
K	2.56	28.96	19.46 (67%)	2.45 (8.5%)	0.88 (3%)	6.17 (21%)
Ca	5.67	82.14	14.75 (18%)	4.75 (5.7%)	0.41 (0.5%)	62.25 (75.8%)
Na	1.92	6.24	2.50 (40.1%)	1.07 (17.1%)	0.28 (4.5%)	2.39 (38.3%)
Mg ^c	0.79		2.45	0.83	0.20	

^aDryfall and wetfall values include estimates for the months of August, September, and October based on mean values for the rest of the year.

^bLitter values were calculated from this years litterfall data and a previous years chemistry of the O₁ litter horizon in late October.

^cNo data available for input of Mg by litterfall at this time.

Fig. 3.35. Seasonal variation in water and mineral input to the *Liriodendron* forest by throughfall, dryfall, wetfall, and stemflow. Stemflow values are means of three collections from three different size tulip poplar trees. Above canopy values taken from one automatically controlled sampler were subtracted from the mean values of three samplers located beneath the canopy to obtain net throughfall values.

collection period, throughfall is about equal to wetfall. another indication of intense rainfall. Wetfall usually exceeded throughfall plus stemflow with an annual input of water to the canopy of 1.23×10^7 liters/ha and an annual input to the forest floor of 1.17×10^7 liters/ha, leaving 0.57×10^6 liters/ha lost by evaporation (and possibly some absorption by the plant tissues).

Current status of the project includes completion of chemical analysis on samples already collected and further analysis and interpretation of data. The first year's data should yield information that will permit the development of equations which will predict input of elements as a function of season and duration and amount of precipitation. Plans include a second year's data collection which will serve as a check on the accuracy of these equations and variations from season to season, and the use of tracers in determining the fate of some of the throughfall elements after reaching the forest floor.

Physical and Chemical Properties of Emory Silt Loam in the Yellow Poplar Experimental Area

This study was undertaken to quantify chemical and associated physical properties of soil in the yellow poplar stand, an intensive research site for IBP studies. Results of this study contributed to synthesis of

preliminary potassium and calcium budgets. Harris²³ has shown that root distribution is concentrated primarily in the upper 60 cm, and this depth was used in calculating mineral soil nutrient pools. Results are included to a depth of 75 cm in this report, however, because of the interesting changes in physical and chemical properties which occur at that depth.

Table 3.17 presents results of profile analyses for organic matter, bulk density, and potassium, calcium, and phosphorus concentrations. The most striking feature of this soil is the decrease in organic matter from 6 to 1.4% at approximately 35 cm, followed by a gradual increase with greater depth. Note also the inverse relationship between bulk density and organic matter with depth. These features are indicative of a "buried soil" profile. The research site is located in a sinkhole with relatively steep (~20%) adjacent slopes. Past land use suggests that these slopes were cultivated with accompanying erosion causing transport of upper soil horizons to the sink for subsequent deposition. Thus the original soil surface was buried under at least 75 cm of soil material which presently constitutes the surface horizons.

The exchangeable potassium content decreases with soil depth and is not influenced by the presence of the

23. W. F. Harris, IBP-EDF Memo Report 71-71 (1971).

Table 3.17. Distribution of soil physical and chemical properties with depth for Emory silt loam in the yellow poplar experimental area

Soil depth (cm)	Organic matter ^a (%)	Bulk density (g/cm ³)	Exchangeable cations ^b (meq/100 g)		Available phosphorus ^c (ppm)	Total	
			K	Ca		K (%)	P (ppm)
0-5	6.01	0.92	0.31	10.6	15.2		
6-10	3.30	1.06	0.33	6.1	9.0	0.53	440
11-15	2.38	1.25	0.30	3.7	6.7	0.50	407
16-20	1.91	1.28	0.23	2.5	7.5	0.56	318
21-25	1.60	1.23	0.20	2.1	6.7	0.56	333
26-30	1.43	1.27	0.19	1.6	7.5	0.51	291
31-35	1.37	1.26	0.18	1.2	12.2		
36-40	1.37	1.17	0.16	1.6	14.0		
41-45	1.90	1.16	0.15	1.2	14.2	0.59	448
46-50	2.30	1.14	0.14	1.2	12.2	0.58	442
51-55	2.43	1.12	0.14	1.6	10.2	0.59	494
56-60	2.43	1.10	0.12	1.9	7.0	0.62	499
61-65	2.97	1.12	0.12	2.2		0.65	490
66-70	2.96		0.10	2.2		0.64	509
71-75	3.06		0.11				

^aBy Walkley-Black procedure as described by Jackson (1958), *Soil Chemical Analysis*, pp. 219-20.

^bExtracted by 1 N NH₄OAc, pH 7.

^cAvailable phosphorus as determined by Bray No. 1, soil-to-volume ratio: 1 g to 20 ml.

buried soil horizon. On the other hand, exchangeable calcium and available phosphorus contents appear to be correlated with soil organic matter content. These results are consistent with the behavior of these elements in soil systems. Potassium is extremely susceptible to leaching and hence would be less likely to be influenced by the buried profile, whereas calcium and phosphorus are strongly influenced by organic matter either in regard to cation exchange capacity or slowly available element forms. Therefore, the distribution of these elements follows the buried horizons. The total potassium content increased slightly with depth. Clay mineralogy analyses have shown greater concentrations of micaceous clays at lower depths, and this is no doubt responsible for the greater potassium content in lower horizons.

Budgets of Ca and K in a *Liriodendron* Forest

Ecosystem budgets for potassium and calcium for the *Liriodendron* stand are presented in Figs. 3.36 and 3.37. Canopy and understory biomass estimates are taken from the Primary Production section of this annual report. Vegetation consists of mesophytic hardwood forest dominated by yellow poplar with several other species including various oaks (*Quercus* relatives, *Q. alba*, *Q. coccinea*, *Q. rubra* and *Q. prinus*), short-leaf

pine (*Pinus echinata*), and hickories (mainly *Carya tomentosa*) attaining canopy height. Understory species include redbud (*Cercis canadensis*), flowering dogwood (*Cornus florida*), and lesser numbers of black gum (*Nyssa sylvatica*), sourwood (*Oxydendron arboreum*), red maple (*Acer rubrum*), and ash (*Fraxinus pennsylvanica*), as well as many hickory saplings. Christmas fern (*Polystichum acrostichoides*) and woody hydrangea (*Hydrangea arborescens*) account for nearly 90% of the herbaceous biomass. The following concentrations (Table 3.18), in addition to those previously reported, were used to calculate mineral pools in vegetation components of the ecosystem.

Nutrient pools in organic soil horizons were calculated from forest floor collections made in conjunction with litter decomposition studies being conducted in the yellow poplar stand. Mineral soil nutrient pools were calculated from data presented in a later section of this report. Canopy and soil invertebrate nutrient contents have been published previously.²⁹⁻³¹ Potas-

29. D. E. Reichle and D. A. Crouley, Jr., pp. 56-87 in *Secondary Productivity of Terrestrial Ecosystems*, Warsaw, 1967.

30. D. E. Reichle, M. H. Shanks, and D. A. Crouley, Jr., *Ann. Entomol. Soc. Amer.* 1969.

31. J. F. McBrayer and D. E. Reichle, ORNL-TM-2847 (1970).

Fig. 3.36. Potassium budget for a yellow poplar stand in Oak Ridge, Tennessee. Pool sizes are presented for July 1970 in kg/ha. Transfer rates are expressed as kg ha⁻¹ year⁻¹.

Fig. 3.37. Calcium budget for a yellow poplar stand in Oak Ridge, Tennessee. Pool sizes are presented for July 1970 in kg/ha. Transfer rates are expressed as kg ha⁻¹ year⁻¹.

Table 3.18. Concentrations (% dry weight) of potassium and calcium in vegetation components

	K (%)	Ca (%)
<i>Liriodendron tulipifera</i>		
Leaves	0.85	1.90
Branches and large roots	0.21	0.38
Bole and stump	0.09	0.21
Other canopy species ^a		
Leaves	1.00	1.30
Branches and large roots	0.18	0.74
Bole and stump	0.13	0.55
Understory species		
Leaves	0.85	1.30
Branches and large roots	0.18	0.44
Bole and stump	0.13	0.47
Herbaceous vegetation	0.30	2.40

^aPredominantly *Quercus* spp., *Oxydendron*, and *Nyssa*.

sium contents in microorganisms are the result of preliminary analyses in conjunction with work on decomposition processes, where system inputs in wet-fall and dryfall as well as transfers from vegetation to the forest floor via throughfall, stemflow, and litterfall also were quantified.

A summary of forest floor and system inputs in conjunction with vegetation uptake of potassium and calcium is presented in Table 3.19. Potassium nutrition must rely on uptake from the mineral soil pool to maintain growth at this stage of development, whereas internal cycling and atmospheric inputs more than offset the calcium uptake requirements. It should be noted, however, that leaching losses have not been accounted for at this stage of our budget development. When these are added the picture may change to reflect mobilization of calcium as well as potassium from mineral soil pools.

These budgets represent an important preliminary step toward our objective of developing models of mineral cycles in forests at both the stand and watershed level of resolution. Within the coming year, preliminary budgets also will be constructed for nitrogen and phosphorus, and more dynamic models of all four elements will be initiated as more transfers are quantified. A major step forward will be achieved as watershed mineral budgets are completed for Walker Branch watershed. These budgets will form the basis for construction of models capable of predicting forest growth and water quality response to management manipulations such as forest fertilization or cutting.

Table 3.19. Summary of annual mineral fluxes in the *Liriodendron* forest ecosystem

	K (kg ha ⁻¹ year ⁻¹)	Ca (kg ha ⁻¹ year ⁻¹)
Total input to forest floor	36.4	85.5
Atmospheric input	5.1	10.5
Amount cycled by biota	31.3	75.0
Leaf uptake	32.9	63.7
Incorporated in wood increment	7.3	20.9
Total uptake by biota	40.2	84.6
Input to forest floor	36.4	85.5
Total uptake by biota	40.2	84.6
Soil loss(-) or gain(+) (without leaching losses)	-3.8	+0.9

REGIONAL STUDIES

J. M. Hett

R. A. Goldstein P. Somers

L. A. Stephens F. G. Taylor

Regional studies are essential if dynamic ecosystem models developed at one point in time are to have either predictive capabilities through time or projective capabilities across the landscape. A regional approach provides necessary information on ecosystem change over a geographic area larger than that encompassed by local forest stands or watersheds. Successional studies give a time depth and history to local studies, while phenological studies indicate how changes in meteorological events from one year to the next influence the timing of events in the ecosystem. Together, these regional process studies provide information on (1) geographic variability of species populations, ecosystems, and watersheds, (2) rates of change through time and resultant changes in biomass or productivity of the region, and (3) the influence of man on these processes, and the response of ecosystems to environmental parameters on a regional basis. Regional process studies provide the basis for extrapolation from specific forest ecosystems to scales comparable with the Deciduous Forest Biome.

The Oak Ridge Reservation, an area which was typical of rural East Tennessee before 1940, offers a unique opportunity for successional and phenological studies. Historical events, such as farm abandonment and forest management practices, are well known, and phenological meteorological observations have been routinely numbered for many years. Three major studies, stand phenology, upland forest succession, and land-use

changes in East Tennessee, have been initiated at Oak Ridge. Each is designed to provide information which will allow broader interpretation of the productivity of local stand and watershed ecosystems at various levels of integration and landscape complexity.

Stand Phenology

During the life cycle of a species, plants undergo a series of distinct life forms or phenophases, which often reflect seasonal climatic phenomena, such as temperature, light, and moisture regimes.³² During the sequence of life forms, biomass, productivity, and nutrient composition change. Thus, phenology reflects the dynamic temporal interactions of meteorology with productivity and mineral cycling processes of ecosystems. The major objectives of the phenological studies at Oak Ridge are to develop phenodynamic spectra for understory and herbaceous species having wide distribution within the Eastern Deciduous Forest Biome, and to correlate (see Terrestrial Primary Production section) meteorological data with dry matter production and nutrient composition at specific phenophases. From the aspect of plant growth and mortality, these short-termed phenophases can be essential to forest mineral cycling models.

Phenophases (leafing out, flowering, fruiting, etc.) reflect developmental stages within the life cycle of a species, plant habitat-group, or community. The number of species within a community actually entering a specific phenophase can be depicted by phenograms (Fig. 3.38) which permit a comparison between spring,

32. H. Lieth and J. S. Radford, *BioScience* 21(2), 62-70 (1971).

Fig. 3.38. A phenogram showing the mean number of 133 species flowering each week between 1963 to 1970 and the number flowering in 1970. January 1 to 7 equals week 1. Two distinct flowering seasons are indicated, one in the spring and the other in the early summer.

summer, and fall floras. In the temperate deciduous forests, the number of species entering the reproductive or flowering phase usually increases rapidly in spring, declines, and subsequently increases again in early summer. This particular phenomenon is not the result of climate, but rather illustrates the presence of distinctively different floras (spring and summer). This phenomenon is related to the leafing-out phase and canopy closure of dominant tree species.

Phenological records of flowering of plant species on the Oak Ridge Reservation have continued since 1963.³³ Since vegetative growth usually diminishes with the onset of the reproductive cycle, phenology of flowering closely parallels periods of maximum biomass and photosynthesis. The resultant phenogram (Fig. 3.38) illustrates that the peak flowering season of the spring component, based on mean flowering date between 1963-70, occurs about the 16th week (April 16-22). A second flowering season, corresponding to the early summer flora, is noted by the 23rd week (June 4-10). A comparison of flowering seasons in 1970 to the 1963-70 mean indicates a one-week delay in spring and a one-week advance in early summer flowering seasons of 1970.

Characterization of the thermal climate by temperature summation techniques (degree days or heat units) has been applied successfully in agrometeorology to

predict dates of flowering, fruiting, and harvest. Similar applications have been used to contrast flowering among species of different microclimates within natural communities. Accumulated degree days or heat units at Oak Ridge during the peak of spring flowering in 1970 was four days later than the date for the same thermal climate (average degree days) between 1963 and 1970. This difference is comparable with the one-week delay in spring flowering season for the same year. Accumulated heat units during peak flowering of the early summer flora (1970) were delayed only one day, whereas date of flowering was enhanced one week.

Expansion of leaves by canopy trees in spring should correspond to the progression of flowering in understory species. Yellow poplar (*Liriodendron tulipifera*) often occurs as a dominant canopy species in local forest ecosystems, and is one of the first woody species to leaf out. The phenology of leaf emergence of this species was recorded during the 1970 season and compared with light extinction at the forest floor (Fig. 3.39). By the end of the 16th week (yearday 112), approximately 60% of the leaves had emerged. This point corresponds to the peak flowering season of the spring flora. By the end of the 22nd week (yearday 154), more than 90% of the leaves had emerged. Current research is emphasizing development of mathematical models relating phenological events to micro-meteorological driving variables.

Upland Forest Succession

Since productivity and other functional aspects of ecosystems change through the course of ecological succession, incorporation of such information into systems models is important to development of regional succession models and to extend the scope of watershed

Fig. 3.39. Cumulative percentage of maximum leaf emergence for *Liriodendron tulipifera* during the 1970 growing season, and concomitant light extinction on the forest floor.

33. F. G. Taylor, "Phenological Records of Vascular Plants at Oak Ridge, Tennessee," ORNL-RP-69-1, 46 pp. 1969.

level analyses to broader geographic areas. A study to investigate the seral or definable sequential stages from pioneer to mature upland oak and/or oak-hickory ecosystems in the valley and ridge province of East Tennessee and the associated productivity for the past five years has been initiated. The regression coefficients³⁴ in Table 3.4 (Terrestrial Primary Production section) were used to calculate temporal sequences of productivity and biomass based on inventories of successional stages.

It has been hypothesized that as succession progresses from pioneer to mature associations, stand structure and species composition change and total biomass increases. Figure 3.40 suggests that this hypothesis is true and that as biomass increases productivity decreases. Sample plots on site 207 have consistently lower biomass than the more advanced successional stages. Transitional stands (205 and 208) are both intermediate-aged and intermediate in biomass, while the most mature stand (203) has the greatest biomass. Correlation of productivity with stand diversity is an important relationship which has yet to be determined.

Gradual replacement of species and their change in biomass also can be seen in Fig. 3.40. Pine which is the dominant pioneer tree species decreases in its relative contribution to the total stand biomass in the transitional stages and becomes a minor component in mature stands. Tulip poplar (*Liriodendron tulipifera*), an understory species in the pioneer stage, increases in the transitional stage to a position of stand codominance and thereafter regresses to a minor component in the mature stands. Initial stand analyses indicate that forest structure, that is, DBH distribution, may convey more important information on successional pathways than species compositional structure. More detailed analyses will attempt to develop functions which

describe successional change based on forest stands with similar structural characteristics. Predictive equations will be developed relating biomass, productivity, and stand structure to a stand's position on the successional sequence.

Land-Use Changes in East Tennessee

The landscape is a dynamic mosaic of natural and man-made or man-influenced ecosystems, each changing as a result of natural processes and/or human impact. It is essential to know the amount of land in each land-use type and rates and direction of change in order to know past and future occurrences and distributional patterns of vegetation. Since man plays an important role in determining the rates and direction of these changes, it is necessary to investigate both where and how his effect on the landscape is being expressed. Changing land-use patterns in the Valley and Ridge Province of East Tennessee (including Rhea, Meigs, Roane, Loudon, and Knox counties) have been completed³⁵ and a simulation model developed which describes these changes for three counties (Rhea, Meigs, and Roane).

For each of the five counties, a 1-km² grid was superimposed over 1939 TVA³⁶ field maps, and the percentage land use in each cell was visually estimated. Nine land-use categories were used: open (primarily

34. W. F. Harris, P. Sollins, and C. D. Monk, "Terrestrial Primary Production at IBP Sites in the Eastern Deciduous Forest," Paper presented at 2nd National Biological Congress, October 23-26, 1971, Miami, Florida.

35. J. M. Heit, Land-Use Changes in East Tennessee and a Simulation Model Which Describes These Changes for Three Counties," ORNL-IBP-71-8, 56 pp, 1971.

36. Division of Forestry, Fisheries, and Wildlife Development, Norris, Tenn.

Fig. 3.40. Biomass in kg/m² of species and stands along a successional sequence of upland sites on the Oak Ridge Reservation. As pine is replaced by hardwoods, biomass increases until it peaks in oak-hickory stands.

Fig. 3.41. The change in frequency of land-use categories for Rhea County, East Tennessee. Open land and hardwood forest show a decrease while all the others have an increase in frequency. The greatest change has been in water and pine response to damming the Tennessee River and the construction of a pine pulp and paper mill in a nearby county.

agricultural land), old field, pine forest and plantations, mixed (conifer and hardwood) forest, cedar-hardwood forest, hardwood forest, water (excluding small streams), urban, and special (a "catchall" including steam plants, quarries, etc.). TVA aerial photographs taken in 1953 were used to collect similar data for Rhea, Meigs, and Roane counties. For the final data set, the most recent photographs available for the five counties were obtained through the cooperation of TVA and U.S.D.A. Agricultural Stabilization and Conservation Service county offices.

Figure 3.41 shows the pattern of change for one of the five counties, Rhea, if the land-use category occupied at least 5% of the area inside the cell, it was

recorded by blocking in the entire cell. Thus, this figure shows the frequency of occurrence. With the exception of open and hardwood forests, all land-use categories show an increase in frequency. Pine forests (probably plantations) and water show the greatest increase. All five counties indicated a shift from open land to forest, water, urban, and special land uses. The annual yearly loss for the five-county unit from nonforest land was $5.28 \text{ km}^2/\text{year}$, of which $2.39 \text{ km}^2/\text{year}$ represented an increase in forested land and $2.85 \text{ km}^2/\text{year}$ was irreversibly lost to water, urban, and special uses. Approximately 160 km^2 of land was lost to water in Meigs, Rhea, and Roane counties, a result of dams built in the Tennessee Valley.

Using the data for Meigs, Rhea, and Roane counties, a simulation model³⁷ (Fig. 3.42) was developed to

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Fig. 3.42. Land-use simulation model showing the nine categories and the direction of change for each component since 1939. The solid lines represent natural successional transfers and the dashed lines those transfers which are man-influenced. Each transfer coefficient is a constant except those indicated as F_5 (constant changed during the fifth year) and F_{14} (constant changed in 1953). See Table 3.20 for transfer coefficient values.

37. Program developed by Philip Sollins, Ecological Sciences Division, Oak Ridge National Laboratory.

Fig. 3.43. Response of each land-use category through time as simulated by the model in Fig. 3.42. The solid points indicate the actual data while the curves show the time response of the land-use category predicted by the model.

investigate both land-use changes and how man influences the rates of these changes. The 1939 data were used as initial conditions for a constant coefficient model, and time-varying coefficients (Table 3.20) were used to account for effects of dams on the Tennessee River and the influence of Bowaters' pine pulp and paper mill on the rate of establishment of pine

plantations. Figure 3.43 shows the results of the simulation model compared with the actual data. The simulation indicates that man's influence on the landscape necessitates a more complex model, for example, pine and water cannot be closely approximated in 1964 unless time-varying coefficients are included.

Table 3.20. Annual transfer matrix (year^{-1}) for the land-use simulation model

All coefficients are constants; changes in coefficient values are approximately indicated:

* = time < 14 years. ** = time > 14 years; † = no transfer; ‡ = transfer occurred only during years 5 and 6.

Category	Open	Old field	Pine	Cedar-hardwood	Mixed	Hardwood	Urban	Water	Special
Open									
Old field	0.0130								
Pine	0.0000* 0.0001**	0.25							
Cedar-hardwood		0.0002							
Mixed			0.1400* 0.0130**						
Hardwood				0.25	0.0029				
Urban	0.0007* 0.0018**								
Water	0.00† 0.1650‡				0.00† 0.02‡	0.00† 0.017‡			
Special	0.00031* 0.0012**								

4. Eastern Deciduous Forest Biome, U.S. International Biological Program

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INTRODUCTION

Stanley I. Auerbach Robert L. Burgess

The role of Oak Ridge National Laboratory in the International Biological Program (IBP) is both large and complex. The Division of Ecological Sciences is central headquarters for the Eastern Deciduous Forest Biome program. This broad research effort is attempting to relate the broad aspects of biological productivity to human welfare. Biological productivity studies investigate the fixation, transfer, flow, and cycling of energy and materials through the complex of nonliving and biotic components of ecosystems, similar in processes, yet differing in organisms and environments in different parts of the world. Knowledge of productivity, including the production of food (both plant and animal), fiber, building materials, etc., is important for man's physical needs, but portions of the earth's surface also furnish living space, scenic vistas, recreational areas, and wildlife habitat as well. These tangential features impinge directly on man's welfare as a burgeoning population places greater and greater pressures on society.

In the eastern United States, the great region of temperate deciduous forest, is a complex of aquatic and terrestrial ecosystems that collectively covers about one-third of the country, but presently supports about two-thirds of the people. In the common, yet unique

situation where land and water systems interface, referred to as a watershed, research is aimed at determining the uptake, transfer, and discharge rates and pathways of critical mineral elements, potential pollutants, and biological materials so that the functioning of the total system, both land and water phases, may be described mathematically in a systems model. Then, by utilization of high-speed digital computers, the mechanics of the ecological system can be simulated. By running such a model for specified lengths of hypothetical time, it is often possible to predict the future outcome of present-day decisions in resource management. The value of such an approach is rapidly coming to be recognized at various levels of government as essential to sound planning and wise resource utilization.

Dr. Stanley I. Auerbach, Biome Director, is assisted by a central management team consisting of Dr. Robert L. Burgess, Deputy Biome Director, Dr. Jerry S. Olson, International Coordinator, Dr. Robert V. O'Neill, Modeling Coordinator, and Dr. F. Glenn Goff, Biome and Regional Analysis Coordinator. From this central group, the integrated research program radiates to five major sites within the biome region: Oak Ridge, using areas and facilities of the USAEC Oak Ridge Reservation, is under the direction of Dr. David E. Reichle, Site Coordinator; other sites include the Coweeta Hydrologic Laboratory of the U.S. Forest Service and the Duke Forest near Triangle Research Park, both in North Carolina, Lake Wingra at Madison, Wisconsin, and Lake George, near Troy, New York.

Funding for this large project is through the National Science Foundation under an interagency agreement with the AEC. Biome management then arranges for subcontract research to be performed at the sites, yet

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coordinated by management so that the ultimate objectives may be reached in the most propitious manner.

TIME-PHASE CHARTING FOR RESEARCH MANAGEMENT

R. V. O'Neill C. Mills³

The integration of large-scale environmental research presents formidable problems in management and information exchange. The Eastern Deciduous Forest Biome, International Biological Program, is managing over 100 research projects at a number of universities spread across the eastern United States. The goals of the program include synthesis of individual research proj-

ects into total ecosystem models. To reach this objective, within the time limitations of the project, it is important that interdependence of individual projects, as well as time phasing of essential interactions, be clearly understood.

To assist in the management of the total program, a graphic technique has been developed to illustrate the time phasing of individual projects, and the synthesis of individual process models into total ecosystem models. Figure 4.1 shows a partial analysis of research interactions within a single site. Eleven individual projects are divided into data collection and data analysis phases. The time phasing of each step in the project can be determined by reference to the time scale at the top of the figure. After preliminary data analysis, the results

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Fig. 4.1. Time-phasing diagram for mineral cycling projects at Oak Ridge National Laboratory IBP Research Site. The interaction and synthesis of 11 projects into an overall nutrient budget model is depicted.

of individual projects are available for synthesis into models, represented by circles on the figure. In addition, data from projects at other research sites will be incorporated into the models. Models in turn will be synthesized into larger-scale models, exemplified by model "NB" in the figure.

While no procedure can be expected to reduce a very complex managerial problem to its simplest form, the time-phasing charts do make synthesis and integration processes explicit. At any point in time, the charts permit management to ascertain the current stage of development for each project and the interactions which should have occurred by that time. The charts thus provide a single instrument for summarizing the complex interrelationships of an integrated research program of the magnitude of the Eastern Deciduous Forest Biome.

BIOME SYSTEMS ANALYSIS AND MODELING

S. I. Auerbach

The development of a total ecosystem model is the responsibility of the biome headquarters modeling group. Total ecosystem modeling has been the subject of intensive thought and discussion since the inception of the biome program. A total ecosystem model deals with terrestrial and aquatic production on the scale of a watershed. On the other hand, our experience indicates that there cannot be a single model which would optimally address every problem. It is likely that more than one general ecosystem model will be produced, and that each would be designed for a single well-defined class of problems. As a result our program is focusing initially on the development of specific process models which will be capable of being linked in various arrays to meet the needs of particular problems. In addition to developing total ecosystem models, the central biome group is responsible for providing technical support in computer sciences and mathematics. During the past year, work has been done on both total models and specific technical aspects of systems analysis. Examples are illustrated in the following section.

A TERRESTRIAL ECOSYSTEM ENERGY MODEL

R. A. Goldstein R. V. O'Neill
H. H. Shugart J. B. Mankin¹

Efforts have been initiated by a team of investigators to formulate a mechanistic model of energy dynamics in a terrestrial ecosystem. Table 4.1 indicates the state variables and energy transfers which will be initially

considered in the model. The model takes the form of a system of differential equations with each transfer represented by a mathematical function. Each transfer is considered to be a function of recipient and donor variables, and of environmental parameters such as solar radiation, temperature, moisture, etc. For present purposes, the system has been divided into vegetation, consumer, and decomposer modules.

The vegetation module considers overstory, understory, and herbaceous compartments. Each compartment is subdivided into leaves, bole, roots, and storage. Bole includes all aboveground biomass that is neither leaves nor labile storage. The forest is assumed to have a closed canopy, and vegetation development is simulated on a daily basis. Photosynthesis is a function of solar radiation, water availability, temperature, and physiological time. Growth is a function of energy stored and past history, as well as temperature, available water, and physiological time.

The consumer module deals with individual groups of terrestrial consumers. Energy consumed is considered the basic input to the population, and excretion, respiration, and predatory and nonpredatory mortality are considered as losses. Multiple food supplies, as well as multiple predators, can be simulated for individual consumer groups. Each input and loss process can be modified by behavioral, physiological, and reproductive mechanisms. In its present implementation, the consumer module considers canopy herbivores, predators and scavengers, insectivorous birds, small mammals, and vertebrate predators as state variables.

The decomposer module operates to decompose an input of materials produced by the other two modules of the model. Bacteria and fungi are considered integral parts of the litter and soil organic variables. Losses from the organic pools are controlled by explicit time functions expressing temperature-moisture responses expected in microbial processes. Microbiotic compartments are expressed by a pair of differential equations: one for the energy pool and another for the number of individuals. The microbiotic components process fresh litter to a different state (old litter) with the associated effects of speeding decomposition.

The completed model should serve as a point of discussion for summarizing our current understanding of the mechanisms operating in the terrestrial ecosystem. Simplifications and elaborations can be made to improve the model for particular applications. By attempting to simulate the total system, the model may prove useful for testing preliminary hypotheses about ecosystem dynamics and for critically examining new experimental designs.

Table 4.1. State variables and interactions for a terrestrial energy model

The "x's" in the table indicate a transfer of chemical energy from the variable listed at the top of the column to the variable listed at the left of the row. Each transfer is represented in the model by a mathematical function.

State variables	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Overstory vegetation																									
leaves	1				x																				
stems	2	x		x	x																				
roots	3		x																						
storage	4	x																							
Understory vegetation																									
leaves	5				x																				
stems	6	x		x	x																				
roots	7		x																						
storage	8	x																							
Herbaceous vegetation																									
leaves	9																								
stems above ground	10	x		x	x																				
roots	11		x																						
storage	12	x																							
Canopy																									
herbivores	13	x				x																			
predators	14												x		x										
supra-canopy	15			x				x																	
Insectivorous birds	16												x		x										
Small mammals	17								x				x		x						x		x	x	
Vertebrate predators	18															x	x				x		x	x	
Fresh litter	19	x	x			x	x		x	x			x	x	x	x	x	x							
Old litter, feces, frass	20												x	x	x	x	x	x	x			x	x	x	x
Soil organic	21																			x					
Fresh litter feeders	22																		x						
Old litter feeders	23																			x					
Cryptosean omnivores	24							x																	
Cryptosean predators	25																					x	x	x	

MODELING OF ENERGY TRANSFER IN A FOREST CANOPY

J. B. Mankir, Jr.¹ C. E. Murphy² K. R. Knoerr³

In order to understand and predict the growth of vegetation, a thorough knowledge of the microenvironment in which plant growth occurs is necessary. Although fluctuations in the water balance frequently dominate the microenvironment, its basic characteristics are determined by the incident solar radiation. Solar energy provides the establishment of a satisfactory thermal environment for proper physiological functioning and a proper light environment for photosynthesis.

Differences between the incoming and outgoing radiation fluxes represent rates at which energy is absorbed by plant and soil surfaces. This energy is dissipated as sensible heat, latent heat, and in metabolic processes. Since metabolic energy normally represents a small fraction of the total energy exchange, most energy transfer between community surfaces and the atmos-

phere is in net exchange of sensible and latent heat. Both exchanges are affected by turbulent eddy movement in the lower atmosphere.

Consider a mature forest stand which is sufficiently flat, homogeneous, and of sufficient horizontal extent to be considered as a one-dimensional heat exchanger. The primary heat exchange surfaces are the soil (or litter) surface and the leaves because of their relatively large surface area. Since the microenvironment is seldom in a steady-state condition, it is desired to determine the nonsteady-state solution for the system of equations describing this process.

If $z = h$ is the height of the top of the canopy and $z = 0$ is the soil (or litter) surface, the process is described by the following system of equations:

$$\frac{\partial T}{\partial t} = \frac{\partial}{\partial z} \left(D \frac{\partial T}{\partial z} \right) + H, \quad (1)$$

$$\frac{\partial q}{\partial t} = \frac{\partial}{\partial z} \left(D \frac{\partial q}{\partial z} \right) + W, \quad (2)$$

where t and z are the time and space variables, respectively. T is the air temperature, q is the air specific humidity, D is the diffusivity, and H and W are source terms which account for sensible and latent heat transfer from the leaves and soil surfaces.

$$\tau_i \frac{dT_{li}}{dt} = \alpha_i(q_{li} - q_i) + \beta_i(T_{li} - T_i) + S_i + R_i \quad (3)$$

where the subscript i indicates the i th layer, T_{li} is the leaf temperature, S_i is the solar radiation, R_i is the long-wave radiation, and τ_i , α_i , and β_i are simplified coefficients of the heat balance equation.

$$S_i = (s - r - t) S_h [\exp(F_{i+1}) - \exp(F_i)] \quad (4)$$

where S_h is the short-wave radiation at the top of the canopy, F_i is an exponent dependent upon the absorbing area of the leaves, leaf angle, and solar attitude, and s , r , and t are the absorptivity, reflectivity, and transmissivity, respectively, of the leaves.

$$R_i = \sum_j G_{ij}(T_{lj}^4 - T_{li}^4) \quad (5)$$

where G_{ij} is a factor representing the fraction of energy radiated from layer j which is absorbed by layer i .

$$D = A_D(z - d)\phi, \quad z \geq h, \\ = D_h \exp[B_D(z - h)], \quad h > z > 0. \quad (6)$$

where D_h is the diffusivity at the top of the canopy and ϕ is a thermal stability correction factor.

$$u = A_u \left[\ln \frac{z - d}{z_0} + \Psi \right], \quad z \geq h, \\ = u_h \exp[B_u(z - h)], \quad h > z > 0. \quad (7)$$

where u is the wind speed, u_h is the wind speed at the top of the canopy, and Ψ is a thermal stability correction factor.

$$\phi = f\left(T, \frac{\partial T}{\partial z}, \frac{\partial u}{\partial z}\right), \\ \Psi = g\left(T, \frac{\partial T}{\partial z}, \frac{\partial u}{\partial z}\right). \quad (8)$$

If the system of Eqs. (1) through (8) can be solved, the temperature and humidity profiles throughout the canopy can be computed.

Equations (1) and (2) are solved using the Crank-Nicolson algorithm by incrementing the time variable by an amount Δt . Equation (3) is solved during the time increment Δt by a Runge-Kutta algorithm. The diffusivity is dependent upon the correction factor ϕ which is dependent upon the wind speed gradient which is dependent on the correction factor Ψ which is dependent upon the wind speed gradient. Therefore, Eqs. (6), (7), and (8) have to be solved simultaneously using an iterative procedure. Equation (5) is solved by summing the radiant energy transfer between the various canopy layers until all the direct solar radiation is accounted for. A modification of this method is used for the diffuse radiation by considering the radiation source to be distributed over several solar attitudes. The diffuse radiation absorbed by each layer can be computed iteratively by summing the contributions from the various radiation sources. These calculations must be performed for each succeeding time increment.

These equations have been implemented in a computer program. Starting with the initial temperature profiles shown in Fig. 4.2, Fig. 4.3 shows the temperature profile after 25 min. The conditions under which this sample calculation is made are an incident direct radiation of $0.7 \text{ cal cm}^{-2} \text{ min}^{-1}$, and a windspeed of 250 cm/sec at the top of the canopy.

Fig. 4.2. Initial temperature profile.

Fig. 4.3. Temperature profile after 25 min.

WATERSHED MODELING

M. Reeves III¹ C. W. Nestor¹
T. C. Tucker¹

The Stanford Watershed Model⁵ has been used quite extensively to simulate water movement through a watershed. Processes such as precipitation, interflow, overland flow, evapotranspiration, soil-water movement, groundwater movement, and channel flow are considered. Given a stream flow hydrograph and the corresponding precipitation records, parameters of the model may be adjusted so that the simulated hydrograph fits the experimental hydrograph. The model can then be used to determine stream flow for any other rainfall event. If the character of the watershed is changed significantly (e.g., land development or reforestation), the model is no longer predictive. These difficulties are being alleviated by describing the soil-water-plant system in more detail.

Topographical effects are being considered through the distributed parameter approach. Such effects are hidden in the lumped-parameter approach of the Stanford Watershed Model but could be important for certain changes in the watershed. Input data will include land use, soil type, and mean slope distributed on a square grid. Such data are now being accumulated by the ORNL-NSF Environmental Project.

The model should take the form of a nonlinear subsystem of first-order ordinary differential equations

coupled together to depict internal flows within an element whose upper surface is one square of the grid mentioned above. These subsystems would then be coupled together by the lateral flows between volumes. By using the ORNL IBM 360/91 and by carefully considering the mathematical form of the couplings, we hope to avoid the excessive execution times reported by Dunn⁶ for a similar model.

INFILTRATION OF WATER INTO SOILS

M. Reeves III¹ E. E. Miller²

A very important process involved in watershed modeling is the division of water between runoff and infiltration occurring at the soil surface during a rainfall. Solution of the soil-moisture flow equation to model such a process is not feasible at present for the space and time scales involved in a typical watershed analysis. The objective of this research is to examine an approximation due to Raats.⁷ By this approach the infiltration for an arbitrary rainfall event may be obtained from the characteristic cumulative infiltration for maximum seepage.

Using an iterative Crank-Nicolson algorithm similar to that used by Whisler and Klute,⁸ we solve the soil-moisture flow equation both for maximum seepage from the surface and for a given rainfall event. The Raats approximation is then compared with the latter result. Hysteresis and a crust are included in the analysis.

Two soils,⁹ Rideau Clay Loam and Caribon Silt Loam, four crusts, and four rainfall events are included in the analysis. For the cases run to date the Raats' approximation is valid to less than about 15%. This error would appear to be acceptable in view of other comparable errors involved in the modeling of a watershed.

EXAMPLES OF ECOLOGICAL TRANSFER MATRICES

R. V. O'Neill

A large number of research ecologists are being exposed to ecosystem modeling techniques in the U.S.

5. N. H. Crawford and R. K. Linsley, "Digital Simulation in Hydrology: Stanford Watershed Model IV," Stanford University Department of Civil Engineering, Technical Report No. 39.

6. D. E. Dunn, "An Experiment in Finite Difference Modeling," Montana State University, 1970.

7. Private communication from P. A. C. Raats to E. E. Miller.

8. F. D. Whisler and A. Klute, *Soil Sci. Soc. Amer. Proc.* 29, 489 (1965).

9. G. C. Topp, *Water Resour. Res.* 7, 914 (1971).

Biome Programs of the International Biological Program. The success of the Integrated Research Program concept depends, in part, on a close working relationship between the modelers and researchers participating in the project. This relationship is enhanced as each member of the team improves his understanding of the other's task. It is not anticipated that every researcher will become an accomplished applied mathematician; however, substantial benefits can be derived from first-hand experience with the behavior and limitations of simple ecological models.

A variety of example models have been extracted from the ecological literature to supplement and implement an existing computer program.¹⁰ By limiting the scope of the effort to linear, constant coefficient models, it was possible to locate 23 pertinent papers. From these papers, 66 matrices were constructed. The availability of this information will, hopefully, encourage research participants to gain experience with simple ecological models.

To simplify the presentation, all matrices were constructed in a similar manner (Table 4.2). Numbers in the matrix represent the fraction of material or energy in a donor compartment that is transferred to a donee compartment per unit of time. In a number of studies, transfer coefficients are given explicitly, and matrices were constructed by a simple process of rearrangement. In the majority of cases, the literature provided only an estimate of total flux, that is, total quantity of material transferred between compartments during an interval of time. The transfer coefficient was then calculated by dividing the total flux by the average standing crop of

the donor compartment to yield a fractional transfer. Coefficients are arranged in the matrix to represent a fractional transfer from the variable indicated by the number at the top of the column to the variable listed to the left of the row.

LINEAR MODELING OF AN ECOSYSTEM

M. Reeves III¹

A computer code has been written to analyze linear ecosystem models. Matrix techniques are used to obtain the solution in terms of the eigenvalues and eigenvectors of the matrix of internal flow coefficients and integrals of time-dependent external forcing functions. Reductions in computer running time of two orders of magnitude have been observed in some cases relative to self-adjusting Runge-Kutta, a finite-difference technique. A discussion of the mathematical and numerical analysis and the input and output may be found in a recent report.¹⁰

LINEAR COMPARTMENTAL ANALYSIS OF ECOSYSTEMS

M. T. Heath¹ R. E. Funderlic¹

A general report¹¹ has been written which discusses the stability or recovery time of linear compartmental

10. M. Reeves III, *A Code for Linear Modeling of an Ecosystem*, ORNL-IBP-71-2 (1971).

11. R. E. Funderlic and M. T. Heath, *Linear Compartmental Analysis of Ecosystems*, ORNL-IBP-71-4 (August 1971).

Table 4.2. Matrix for global exchange of carbon (Bolín 1970)^a

Variables refer to total quantities of carbon on the earth's surface (year⁻¹).

Variables		1	2	3	4	5	6	7	8	9
Atmosphere	1	-1.93E-1	2.22E-2	3.57E-2	1.94E-1					2.50E-7
Terrestrial plants	2	5.00E-2	-7.78E-2							
Terrestrial dead organic	3		5.56E-2	-3.57E-2						
Marine surface water	4	1.43E-1			-3.54E-1			1.17E-2	1.30E-3	
Phytoplankton	5				8.00E-2	-8.00E00				
Zooplankton and fish ^b	6					4.00E00	-6.67E00			
Marine dead organic	7					4.00E00	6.67E00	-1.37E-2		
Marine deep water	8				8.00E-2			1.67E-3	-1.30E-3	
Sediments	9							3.33E-4		-2.50E-7

^aStanding crops and fluxes from figure on p. 130 of B. Bolín, *Scientific American* 223(3), 124-46 (1970).

^bStanding crop taken as 2 billion metric tons.

models of ecosystems. These models can be expressed as a system of differential equations

$$\dot{x} = Ax,$$

where $A = (a_{jk})$ is the matrix of transfer coefficients and x is the vector of concentrations in the compartments. Theorems are stated in the report which could be of value in investigating such systems, and indications are given for further research in this area. More specifically, the information sought is a certain eigenvalue of the matrix A . Of course, the eigenvalue could be calculated by a computer program, but this might not yield insight into the structure of the system and how changes in system parameters affect this crucial root. For this reason, simple bounds are given for the eigenvalue in question, and a procedure is outlined for determining its value more exactly if needed (under certain conditions of the matrix).

AN ECOSYSTEM EIGENVALUE SENSITIVITY PROGRAM

R. E. Funderlic¹

A preliminary computer program has been written which calculates the partial derivatives of the eigenvalues of a matrix with respect to changes in the matrix elements. In a linear compartmental model of an ecosystem, these derivatives reflect the sensitivity of the stability or recovery time of the system to changes in its transfer coefficients. All such derivatives have been calculated for the 66 matrices which appear in a recent report.^{1,2} Investigation is under way to find trends among these which would be helpful in understanding the stability of ecosystems.

POOLS OF RAPID AND SLOW TURNOVER OF ORGANIC CARBON IN THE BIOSPHERE

J. S. Olson

International and inter-biome coordination for the International Biological Program has had a continuing goal of evaluating data that are available to modeling productivity and cycling of elements. Part of the 1970 SCEPT study,^{3,4} provided some quantitative measures of

several different kinds of interference by man with carbon's natural biogeochemical cycle which integrates and maintains productivity of local and global ecosystems (see Systems Ecology). In some degree the assimilation of organic matter in the biosphere compensates for some of the excess carbon dioxide which is released by burning of fossil fuels in the atmosphere. Yet, land clearing is releasing much carbon from trees and humus.

One of the conclusions from synthesis in IBP research^{1,3,14} is that terrestrial plants may absorb substantially more carbon by photosynthesis than do organisms in the ocean or other aquatic systems. Some of this organic carbon is returned to the medium (air or water) very rapidly as respiration and, by definition, is not even counted in net primary production estimates of Table 4.3. In principle there is a continuum of residence times among other organic products, but Table 4.3 partitions them conveniently into components with "short" and "long" residence times. On land the former have residence times averaging less than three years; reciprocals of residence time give a mean turnover fraction near 0.38. By contrast, materials of long residence time, trees and dead materials with a moderately long residence time (e.g., most humus, but not coal), are taken together as having turnover coefficients averaging near 0.016. Only moderate variation around this value is indicated among the major classes of terrestrial ecosystems, but much local variation exists within biomes. In aquatic ecosystems the terms are known much more poorly, but the present summary treats "short-lived" components (e.g., mostly plankton) as having a mean turnover at least an order of magnitude faster than the equivalent category for land. Stable organic by-products are considered by some as having more than an order of magnitude slower turnover (Table 4.3).

Carbon dioxide is exchanged with the oceans through the buffered carbonate system, which formerly was thought by many to be chiefly responsible for controlling atmospheric CO₂ content. These physical-chemical exchanges plus the total carbon for the marine biosphere and the short-lived and long-lived totals for the terrestrial biosphere have been considered to date in successive carbon budget calculations carried out at

12. Robert V. O'Neill, *Examples of Ecological Transfer Matrices*, ORNL-IBP-71-3 (June 1971).

13. Study of Critical Problems of the Environment (SCEPT), "Man's Impact on the Global Environment: Assessment and Recommendations for Action," M.I.T. Press, Cambridge, Massachusetts, 1970.

14. J. S. Olson, "Carbon Cycle and Temperate Woodlands," chap. 15 in *Ecological Studies I. Analysis of Temperate Forest Ecosystems*, ed. by D. E. Reichle, Springer-Verlag, Berlin-Heidelberg-New York, 1970.

Table 4.3. Biospheric carbon budget estimates: income, inventory, and loss terms^a

Ecosystem complex	Net primary production ^b (10 ⁹ metric tons/year)			Organic carbon pools (10 ⁹ metric tons/year)			Turnover fraction (year ⁻¹)	
	Residence time			Residence time			Residence time	
	Short ^c	Long ^d	Total	Short ^c	Long		Short	Long
					Live ^d	Dead ^d		
Land communities								
Forest, woodland	20	16	36	62	420	530	0.3226	0.01684
Wetlands, thickets	1	0.8	1.8	1	4	25	1.0	0.02759
Grassland, tundra	4.2	4.8	9.0	11	26	275	0.3818	0.01584
Desert, semidesert	1.8	1.4	3.2	4	16	39	0.45	0.02545
Agricultural, urban	4	2	6	4	11	150	1.0	0.01242
Subtotal	31	25	56	82	470	1019	0.378	0.01667
Aquatic communities	21	1	22	2	1.3	700	10.5	0.00142
Global (organic) ^e			78	84	473	1719		
Atmospheric				683				

^aExcludes incipient fossil fuels and slow exchanges with lithosphere, and resistant humus or peat decaying with turnover fractions of the order of 0.001/year or less.

^bIntegrated annual rates of photosynthesis minus respiration of all parts of live green plants.

^cIncludes leaves, green litter, and animals of short residence time before return of carbon to the atmosphere.

^dResistant materials of live plants, including heartwood plus long-lived animals.

SCEP¹⁵ and provided to L. Machta for contributions to the SMIC study.¹⁶

While some economically important components of the oceanic biota are being affected by man's impact, the change in total ecosystem function is not likely to be prompt. On land, however, current efforts to reconstruct the impact man has already had on terrestrial ecosystems suggests a large historic change in the world's carbon budget. Future changes, related to population per unit area and resource use per capita, pose relatively more immediate problems for regulating the function of land ecosystems than oceanic systems. Many of these impacts have received much local attention and some protest from the public. Evaluating their cumulative effects over a region as large as the Eastern Deciduous Biome or the United States, much less the world, is a challenge that is only being carried to the "demonstration" stage to help judge how workable large-scale modeling is likely to be in the future. In the particular case of the carbon cycle, the mixing within the global atmosphere as a whole makes

any future evaluation rather strongly dependent upon the existing situation and trends outside the boundaries of any one nation.

STEADY-STATE PHOTOSYNTHESIS MODEL

R. A. Goldstein J. B. Mankin

We are currently developing a steady-state leaf photosynthesis model which applies energy, carbon, and water balances to a leaf. For specified environmental conditions and general physiological and morphological characteristics of the leaf and plant to which the leaf is attached, the model calculates Ψ_L , leaf water potential; T_L , leaf temperature; and C_L , carbon dioxide concentration at the carboxylation sites. From the above variables, the model calculates rates of net photosynthesis and transpiration.

The energy balance stipulates that the rate of energy absorption by the leaf of solar plus long-wave radiation equals the rate of energy emission by the leaf through the processes of radiation, transpiration, and convection.

$$\alpha S + 2\epsilon R = 2\epsilon\sigma T_L^4 + L_V \frac{\rho_{VL} - \rho_{VA}}{r_A + r_s} + 2\rho_A C_p \frac{(T_L - T_A)}{r_A}, \quad (1)$$

15. J. Machta, C. D. Keeling, and J. S. Olson et al., in SCEP (op. cit.), pp. 46-55, 82-88, 160-66, 192-200, 244-47, 1970.

16. Study of Man's Impact on Climate (SMIC), *Inadvertent Climate Modification*, M.I.T. Press, Cambridge, Massachusetts, 1971.

where

a = fraction of solar radiation absorbed by leaf.

S = intensity of solar radiation (energy/area time).

ϵ = emissivity of leaf.

R = intensity of long-wave radiation (energy/area time).

σ = Stefan Boltzmann constant.

T_L = leaf temperature.

L_v = latent heat of vaporization (function of T_L).

ρ_{VL} = saturation water vapor density at mesophyll surface (function of T_L).

ρ_{VA} = water vapor density of atmosphere.

r'_A = boundary layer resistance to flow of water vapor (function of wind velocity and leaf size).

r'_S = stomatal resistance to flow of water vapor (function of C_L and Ψ_L).

ρ_A = density of air (function of temperature and water vapor content).

C_p = specific heat of air at constant pressure (function of water vapor content).

r_A = boundary layer resistance to diffusion of heat (function of wind velocity and leaf size).

Those processes that take place on both surfaces of the leaf are multiplied by two. The leaves we are interested in only have stomata on the abaxial surface.

The carbon balance stipulates that the rate of diffusion of carbon to the carboxylation sites is equal to the net rate of photosynthesis.

$$\frac{C_A - C_L}{r''_A + r''_S + r''_M} = \frac{1}{(1/\epsilon_1 a S) + (1/\epsilon_2 C_L)} f(T_L), \quad (2)$$

where

C_A = carbon dioxide concentration of atmosphere (function of T_A and ρ_A).

C_L = carbon dioxide concentration at carboxylation sites.

r''_A = boundary layer resistance to diffusion of CO_2 (function of wind velocity and leaf size).

r''_S = stomatal resistance to diffusion of CO_2 (function of C_L and Ψ_L).

r''_M = mesophyll resistance to diffusion of CO_2 .

ϵ_1 = maximum efficiency of utilization of absorbed solar radiation in photosynthesis.

ϵ_2 = maximum efficiency of utilization of CO_2 in photosynthesis.

$f(T_L)$ = function giving effect of leaf temperature on net rate of photosynthesis.

The water balance stipulates that the rate at which water vapor is leaving the plant equals the rate at which water is flowing from the soil to the leaves.

$$\frac{\rho_{VL} - \rho_{VA}}{r'_A + r'_S} = \frac{\Psi_{SO} - \Psi_L}{\alpha r''_{SO} + r''_P}, \quad (3)$$

where

Ψ_{SO} = soil-water potential.

Ψ_L = leaf-water potential.

α = ratio of transpiration area of plant to effective water conducting area between roots and soil.

r''_{SO} = resistance to movement of water between roots and soil (function of Ψ_{SO}).

r''_P = resistance of plant to movement of water.

The water balance differs from the energy and carbon balances in two major respects. Most often, it takes only minutes for a leaf to come into equilibrium with its environment in terms of carbon and energy, while it takes hours to reach a steady state in terms of water transport through the plant. While conceptually it is perfectly acceptable to isolate a single leaf and impose a carbon and energy balance, water uptake by the plant from the roots will be dependent on the transpiration of the entire plant canopy. The environment and physiological properties of the leaves throughout the canopy are in most instances not uniform. Hence, the water balance appears to be conceptually weaker than the other two balances within the framework of the model; however, for the objective of estimating relative effects of environmental and plant parameters on photosynthesis in order to identify the major variables and mechanisms, this weakness is not considered significant. Plant-water relations is an area requiring considerably more intensive research.

Figures 4.4–4.6 illustrate the application of the model to an abstract plant. The plant is an abstraction because the parameters used to describe it are based on values we found scattered throughout literature for several different plants. We are presently in the process of replacing many of these values with others based on experiments performed by our colleagues. The figures show the variation in leaf temperature, net photosynthesis rate, and transpiration rate as a result of

Fig. 4.4. Leaf temperature, net photosynthesis rate, and transpiration rate as functions of relative humidity.

Fig. 4.5. Leaf temperature, net photosynthesis rate, and transpiration rate as functions of air temperature.

Fig. 4.4. Leaf temperature, net photosynthesis rate, and transpiration rate as functions of solar radiation.

varying a single parameter and holding the other parameters constant. The environmental conditions for all cases (unless otherwise stated) are atmospheric temperature = 27°C , relative humidity = 80%, soil water potential = -2 bars, and wind speed = 100 cm/sec.

In Fig. 4.4, relative humidity is varied from 10 to 100%, and the leaf temperature increases 4° . The net photosynthesis rate increases approximately 27%, while the transpiration rate decreases about 82%. All changes are approximately linear. The increase in water use efficiency, measured as the ratio of the net photosynthesis to transpiration, is over 600%.

In Fig. 4.5, air temperature is varied from 22 to 32°C . The water vapor density of the air is held constant to its value at 27°C , 80% relative humidity. Hence, the relative humidity of the atmosphere varies, but the water vapor content remains constant. The leaf temperature increases approximately linearly from 24 to 30°C . The net photosynthesis increases about 40% and is leveling off at about 32°C air temperature. If the air temperature were further increased, the net photosynthesis would be expected to start decreasing. The transpiration increases about 130% in an approximately linear fashion.

In Fig. 4.6, solar radiation is varied from 0.000 to $0.020 \text{ cal cm}^{-2} \text{sec}^{-1}$, and leaf temperature increases about 6° in a linear fashion. Transpiration also increases linearly by 42%, and the rate of net photosynthesis increases from 0 to $0.248 \text{ g CO}_2 \text{cm}^{-2} \text{sec}^{-1}$.

5. Systems Ecology and Environmental Systems Analysis

R. S. Booth ¹	S. V. Kaye	C. W. Nestor ²	P. S. Rohwer ⁴
O. W. Burke ¹	J. B. Mankin ²	R. V. O'Neill	H. H. Shugar ¹
R. E. Funderlic ²	E. E. Miller ³	J. S. Olson	P. Sollins
R. A. Goldstein	C. E. Murphy ³	M. Reeves III ²	T. C. Tucker ²
M. T. Heath ²			

The Systems Ecology Program spans a wide range of activities within the Ecological Sciences Division. Contributions from individual analysts are to be found in a number of other sections of this report. As the Division programs expand and the relatively young modeling staff develops experience and expertise, their contributions become virtually indistinguishable from the research and programs within which they operate. Collected in this section of the report are those contributions which represent specific advances and applications in the field of environmental systems analysis.

GENERALIZED TERRESTRIAL FOOD PATHWAY MODEL

R. S. Booth S. V. Kaye P. S. Rohwer

Major attention has been focused on modeling the important environmental pathways leading to intake of radioactivity via ingestion of food and drink. One phase of this work is represented by the flow diagram in Fig. 5.1 which shows the terrestrial food pathways included in one of the ORNL systems analysis computer codes.⁵ The three *S*'s in Fig. 5.1 are adjusted to reflect initial partitioning of the source, *F*, among the three primary interceptor compartments: deposition directly on the surface of the edible parts of food crops, deposition on cropland soil, and deposition on pasture grass. Movement of radioactivity from one compartment to another is quantified by the *r*'s, known as environmental transfer coefficients. This diagram shows that man ingests radioactivity via consumption of surface-contaminated food crops, crops contaminated via root uptake, beef, and milk. The *d* factors adjust for radioactivity lost in harvesting and food preparation, as well as dietary characteristics of the populations ex-

posed. Total daily intake as a function of age and time is the output of the environmental systems analysis and serves as input, in conjunction with the other data, for the two codes computing the dose estimates.

The terrestrial food pathway model diagrammed in Fig. 5.1 was used in a detailed study of the dynamics of 25 radionuclides.^{5,6} A sample output shown in Fig. 5.2 illustrates predicted intakes by man from an initial impulse deposition of 1 pCi/cm² of each of seven radionuclides in the receptor compartments. These same radionuclides are shown in Fig. 5.3 in terms of the dose to the total body of a standard man consuming a reference diet composed of the four food items. Although analysis of our intake estimates reveals that ⁹⁰Sr constitutes 5% and ²⁰⁴Tl constitutes 25% of the total intake (pCi) during the first 120 days following environmental deposition, those two radionuclides contribute 55 and 1% of the estimated total dose commitment (seven radionuclides) for the total body, respectively. If we consider dose-commitment accumulations in the critical organs for those two nuclides only, ⁹⁰Sr contributes over 97% of the total dose commitment for bone and ²⁰⁴Tl contributes nearly 45% of the total

1. Instrumentation and Controls Division.

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3. Consultant.

4. Health Physics Division.

5. R. S. Booth, S. V. Kaye, and P. S. Rohwer, *A Systems Analysis Methodology for Predicting Dose to Man from a Radioactively Contaminated Terrestrial Environment*, USAEC CONF-710501 (in press).

6. R. S. Booth and S. V. Kaye, *A Preliminary Systems Analysis Model of Radioactivity Transfer to Man from Deposition in a Terrestrial Environment*, ORNL-TM-3135 (October 1971).

ORNL-DWG 70-11733A

Fig. 5.1. Block diagram of the generalized terrestrial food chain model for all radionuclides. .. Capital computer code is used to predict man's intake rate ($\mu\text{Ci}/\text{day}$) of each radionuclide cycled through this system.

for the gastrointestinal tract. These results emphasize that when one attempts to identify "critical" radionuclides it is important to evaluate the radionuclide release on the basis of radiation dose rather than on picocuries ingested. Curves rapidly approaching their asymptotic values in Fig. 5.2 identify those radionuclides having short radioactive half-lives and/or environmental half-times.

The conclusions drawn from this hypothetical release are specific to the mix of radionuclides, the modeling schema, and the initial conditions specified. The relative quantities of the various radionuclides present in an actual radionuclide release could influence significantly the outcome of analyses such as these presented here. Topology changes and site specific data would be used in applying this model to a selected site. Wherever possible the dynamics of this general-purpose terrestrial food pathway model were checked against measurements from specially designed experiments or monitoring of worldwide fallout. In some instances these

comparisons led to programming more detailed models of the abbreviated subsystems in Fig. 5.1. Examples of some of these more detailed models are given in the following section.

DYNAMICS OF THE FORAGE-COW-MILK PATHWAY FOR TRANSFER OF RADIOACTIVE IODINE, STRONTIUM, AND CESIUM TO MAN

R. S. Booth O. W. Burke S. V. Kaye

A systems analysis model was developed to predict transfer of radioactive iodine (Fig. 5.4), cesium, and strontium (Fig. 5.5) from air above a pasture into milk and meat produced by cattle. The system was represented by a series of compartments coupled by transfer coefficients, thereby forming pathways from the initial air concentration to the milk and meat compartments. Equations written for the compartments were solved with an analog computer.

where

β_{nk} = percentage of 30-year intake (summed over all pathways) accumulated at time t by the i th radionuclide in the k th pathway.

$I_{nk}(r)$ = intake rate ($\mu\text{Ci/day}$) of the n th radionuclide in the k th pathway at time r , and

$\Sigma_k I_n(\tau)$ = summation of intake rates of the n th radionuclide over all pathways at time τ .

Fig. 5.3. Contribution of each radionuclide to dose commitment (rem) predicted for total body during the first 120 days following deposition of 1 pCi/cm² in the environment.

There are three systems in the model: the cow system ($Q_1, Q_2, Q_3, Q_4, Q_5, Q_6, Q_7, Q_{13}$), the grass-soil system (Q_8, Q_9, Q_{10}), and the water supply system (Q_{11}, Q_{12}). Model equations are based upon a radioactivity balance within each compartment. Thus, every transfer from a given compartment must be a transfer to another compartment except for loss by radioactive decay. Mass-balance equations were also used to conserve mass. The general form of the equation used to estimate the amount of radioactivity in the n th compartment is

$$\dot{Q}_n = F_n + \sum_{\substack{m=1 \\ m \neq n}}^m \lambda_{n,m} Q_m - \lambda_n Q_n \quad (1)$$

The term F_n is the fallout source to the n th compartment with units of microcuries per square meter per

day. The symbol Q_n represents the amount of radioactivity in the n th compartment in units of microcuries per square meter for the grass and surface water compartments and units of microcuries for all others ($\dot{Q}_n$ is the time derivative of Q_n). The expression $\lambda_{n,m} Q_m$ is the transfer rate from the m th compartment to the n th compartment and $\lambda_{n,m}$ has units of (days)⁻¹.

The transfer coefficients $\lambda_{m,n}$ are independent of the radioactive decay of the isotope under study. Once the $\lambda_{m,n}$'s are determined and λ_R is fixed by the selection of a particular isotope, then the λ_n 's are also determined. Thus, the λ_n 's are a convenient collection of transfer coefficients.

The radionuclide concentrations in various compartments were determined for two cases. The first case was the impulse response of the cow, since an initial concentration of radioactivity was assumed to be present in the cow gut, with all other compartments initially free of radioactivity. In the second case, a concentration of radioactivity was above the pasture for a short time, resulting in an initial concentration of $6 \times 10^3 \mu\text{Ci}/\text{m}^2$ on the grass. This case simulated the passage of a contaminated cloud over the pasture, and it is the impulse response of the entire system. Radionuclide concentrations in the grass, gut, blood, milk, and reservoirs are presented for ^{131}I , ^{137}Cs , ^{90}Sr , and ^{90}Sr as a function of time after introduction of the radioactivity. Results for ^{90}Sr and ^{90}Sr are illustrated in Fig. 5.6.

Several general conclusions were reached from the results of these two cases. Transfers of radioactivity from grass to gut, gut to blood, and blood to milk were very rapid, and transient equilibrium was established in these compartments within a few days after input to the grass. For ^{131}I input to the grass, for example, the milk concentration was a constant times the grass concentration after about five days. This rapid transfer to milk was further illustrated when radioactivity was initially added to the gut, since the gut was emptied of radioactivity within a day or so and the dynamics of the milk compartment practically duplicates that of the blood.

Uptake and subsequent loss of radioactivity by the body reservoirs was evident in the milk concentrations because the reservoirs are feedback paths to the blood and the blood activity is mimicked by the milk. For example, the ^{137}Cs concentration in milk about 30 days after input on the grass is primarily determined by the transfer of radioactivity from meat to blood to milk rather than the direct transfer from grass to blood to milk.

ORNL-DWG 70-8008AR

Fig. 5.4. Block diagram illustrating the transfer of iodine through the fallout-cow-man food chain.

ORNL-DWG 71-10282

Fig. 5.5. Block diagram illustrating the transfer of strontium and cesium through the fallout-cow-man food chain.

Fig. 5.6. Radiocesium concentrations in several compartments of the model for ^{137}Cs and ^{134}Cs vs time after an initial concentration in the gut and in the grass.

Neglecting the cow's body reservoirs in estimating radionuclide uptake by man after an initial deposition on the grass would result in underestimating the total transfer because (1) the meat and soft tissue (which includes the liver and heart) are consumed by man, and (2) the reservoirs continue to transfer radioactivity to milk long after the radioactivity has essentially disappeared from the grass.

As a preliminary test of the model, selected predictions were compared with a limited number of available measurements. For example, the ratio $\mu\text{Ci/kg meat} \div \mu\text{Ci/liter (milk)}$ agrees with published values within a factor of 2 except for strontium transfer to milk. This agreement, which tends to validate the model, cannot be considered conclusive since the single set of parameters used in the model may not apply where the measurements were made. That is, exact and complete testing of the model can only be done if the experimental conditions during the measurement are used to specify the input data for the model simulation.

A TWO-COMPARTMENT, THREE-PARAMETER MODEL FOR THE ABSORPTION AND RETENTION OF INGESTED ELEMENTS BY ANIMALS

R. A. Goldstein J. W. Elwood

In many experiments on absorption and retention of ingested elements, the measured retention curve is fitted to the sum of two exponential functions. The model used most often to interpret results assumes that the instantaneous rate of absorption is proportional to the instantaneous rate of ingestion. The authors have proposed⁷ a model that assumes the instantaneous rate of absorption is proportional to the amount of unabsorbed element in the gut. The models lead to different interpretations of the parameters of the retention curve and to different functional descriptions of the accumulation of absorbed element in the body. Data are presented to support the author's proposed model over the commonly used model. Since both models are of equal mathematical complexity, there is no justification for favoring the commonly used model.

Figure 5.7a shows the commonly used model and Fig. 5.7b shows the model we propose. The differential equations describing the dynamics of the first model are

$$\frac{dG(t)}{dt} = p_1 i(t) - k_1 G(t), \quad (1a)$$

$$\frac{dB(t)}{dt} = p_2 i(t) - k_2 B(t). \quad (1b)$$

Fig. 5.7. Two compartment, three-parameter models for the retention of ingested elements by animals. (a) Model commonly used, (b) model proposed by authors.

The differential equations describing the dynamics of the second model are

$$\frac{dG(t)}{dt} = i(t) - (u + k_1)G(t), \quad (2a)$$

$$\frac{dB(t)}{dt} = uG(t) - k_2 B(t), \quad (2b)$$

where G is the amount of unabsorbed element in the animal's gut; B is the amount of absorbed element in the animal's body; u , k_1 , and k_2 are functions for absorption, unabsorbed element elimination, and absorbed element elimination, respectively; p_1 and p_2 are amounts of element per unit of ingested element transferred to compartments G and B , respectively ($p_1 + p_2 = 1$); and $i(t)$ is the rate of elemental ingestion. We are treating the parameters u , k_1 , k_2 , and p_1 as constants. We recognize, however, that these parameters are functions of various physical, chemical, and biological conditions.

Figure 5.8 shows the percentages of ingested element in the body compartment B after a single feeding

7. R. A. Goldstein and J. W. Elwood, *Ecology* 52, 935-40 (1971).

Fig. 5.8. Percentage of ingested element in the body compartment B after a single feeding according to first (dashed line) and second (solid line) models for two different cases.

according to the two models for two sets of parameters. The feeding occurs at time zero, and we assume that ingestion occurs over a period of time t such that

$$t \ll \frac{1}{k_1},$$

$$t \ll \frac{1}{k_2},$$

and

$$t \ll \frac{1}{u}.$$

We also assume that the initial concentrations of element in the body and gut are 0.

ERROR ANALYSIS OF ECOLOGICAL MODELS

R. V. O'Neill

Systems analysis techniques are valuable in the analysis of radionuclide kinetics in ecosystems. However, the art of systems modeling is relatively new to ecology, and few guides are available for constructing

ecological models. As a result, untested hypotheses are sometimes involved in model development. For example, it may be difficult to predetermine optimal model complexity, that is, the number of state variables or compartments to be included in a model for acceptable accuracy. It could be argued that a more complicated model can account more accurately for complexities in the real system. While this argument appears correct intuitively, additional factors need to be considered.

The hypothesis that greater complexity leads to greater accuracy was tested by analyzing the total uncertainty accompanying a model prediction. In general, systematic bias, resulting from abstracting the system into a few variables, is inversely related to complexity (Fig. 5.9). However, there is a concomitant increase in uncertainty due to measurement errors on individual model parameters. As more parameters are added to the model, they must be quantified in field and laboratory experiments which are never error-free. If these measurement errors are promulgated through a simulation, they contribute to uncertainty in model predictions. By applying Monte Carlo simulation techniques, it was possible to account explicitly for each component of the total uncertainty. Particular atten-

Fig. 5.9. Components of error on model predictions as a function of model complexity. Systematic bias or alpha error is usually assumed to decrease as models account for more of the complexities of real systems. Measurement or beta error might be expected to increase as more parameters are added to the model. The resultant model inaccuracy or gamma error ($\gamma = \alpha + \beta$) may, therefore, tend to increase for very complex models. The shape of the three curves and the relationships between them illustrate the hypotheses examined in this study. The relationships suggest that there is an optimal level of complexity for a model.

tion was paid to the balance between systematic bias and measurement errors. This analysis indicated that the gain in precision from increasing model complexity is not as consistent an outcome as might be expected. Results appear valid for a wide range of modeling applications.

ECOLOGICAL SYSTEMS AND TECHNOLOGY ASSESSMENT

J. S. Olson

As part of its long-range planning, the Ecological Sciences Division is assessing priorities of its environmental research that also bear on broad AEC mission responsibilities. This complements our work with the Health Physics Division on environmental assessment of dose to man. Additional impacts of nuclear technology on various environments on which man depends include several categories in terms of urgency: (1) Impacts around individual nuclear facilities have received direct attention in 1971 from many of the Division's staff. (2) The ecological impacts (e.g., thermal, chemical) which could not be well evaluated because of missing information or insufficient allowance for system interactions have also been reviewed with regard to model efforts in future years of the Division's research. (3) This leaves a number of other problems that are recognized as having a longer delay before humans are affected, unknown probabilities for the magnitude of perturbing influences, and for uncertain ecological effects and costs resulting from such influences.

At the request of the AEC's Division of Biology and Medicine, the Ecological Sciences Division contributed to the Massachusetts Institute of Technology's "Study of Critical Environmental Problems" (SCEP) in 1970 to place several of these matters in perspective. Facts and projections on several problems (energy by-products, other pollution, ecological effects, land use, and climate) have been organized before, during, and after that study. Several crude indices of "ecological demand" or impact on man's environment are expanding at rates considerably higher than energy use, for example, 5 to 6% or more per year in developed and developing countries. Illustrative case studies included DDT, mercury pathways, petroleum at sea, and phosphorus cycling (technological more than ecological). These examples and briefer review of additional sensitive areas confirm that not all the public alarm about such problems is exaggerated. The instantaneous danger is not necessarily overwhelming, but the lag factor inherent in implementing realistic control poses social

problems which have been widely discussed in environmental literature.

As one illustration centrally related to AEC's energy research, initial work with SCEP was with the group on "Energy Products" which added to and evaluated the M.I.T. staff's estimates of present and future emissions of wastes or their "residual" effects.⁸ Effluents were calculated first, accepting AEC projections and several others using closely related extrapolative techniques. Most concern and doubt from the leaders of the SCEP study remained about the environmental by-products of the nuclear alternatives to the present sources of electric power of the national and world economy.

For baseline reference, the group accepted AEC's 1969-1970 projections of installed nuclear generating capacity and total power capacity. One concern was the implication of these projections for growth of fossil fuel effluents; another concern not fully reflected in the SCEP report was with the alternatives (particularly for CO₂ and the ecology of the carbon cycle) of growth patterns for nuclear power which might be either lower or higher than those taken as a baseline.

On the low side, a lag was evident already by late summer 1970 and was then foreseen as likely to be extended somewhat by procedural requirements of the 1969 National Environmental Policy Act (NEPA). Compared with the approximate baseline estimate of 1.43×10^9 tons of CO₂ for 1970 and 2.16×10^9 tons for 1980, a reduction to, say, half the projected 1980 nuclear operating capacity would either increase the CO₂ emission rate near 2.5×10^9 tons or else start slowing down the total electric generating capacity growth on a national or international scale.

Everyone realizes that projections to 2000 AD are subject to many frailties. If the total capacity projections for that year still held, CO₂ effluent rates would approximate 5.24×10^9 tons/year with a "low" nuclear operating capacity of 0.6×10^6 MW(e); 4.87×10^9 tons/year for a capacity of 0.67×10^6 MW(e) (AEC's 1969 projection without a major breeder program); a significant but unknown amount below these rates with stronger nuclear programs (with breeders). Any such levels imply a significant change in the global and regional carbon cycles, and hence in many ecosystem production models of the sort noted under the Biome Applications section of this report.

8. E. Hamilton, John Franklin, J. Olson, et al., "Working Group on Energy Products," pp. 288-306 in *Man's Impact on the Global Environment* (Study of Critical Environmental Problems, SCEP), M.I.T. Press, Cambridge, Massachusetts, 1970.

Whether the climatic influence of CO₂ is as great as some groups expect or is counteracted by other influences like turbidity, it is important that the opposing and shifting tendencies toward change be evaluated.⁹ Energy generating at the levels projected within the present century will be imposing local thermal effluent problems far more severe than our Division has had to consider in connection with current

environmental impact statements; the possibility of broader regional and global disturbance of climatic balance calls for ecosystem modeling in advance of the environmental change instead of concurrent with it.

9. "Inadvertent Climate Modification," *Study of Man's Impact on Climate (SMIC)*, M.I.T. Press, Cambridge, Massachusetts, 1971.

6. Radiation Effects in Terrestrial Ecosystems

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EFFECTS OF FIELD FALLOUT RADIATION DEPOSITS ON REPRODUCTIVE CAPACITY OF FESCUE

R. C. Dahlman Y. A. Tanaka J. J. Beauchamp

Reproductive response of plants in a regime of chronic, low-level, beta-gamma in situ radiation was determined for simulated fallout contamination in the ¹³⁷Cs grassland facility. Observations were made on the effect of combined internal-external irradiation on seed production and germination of Ky-31 tall fescue (*Festuca arundinacea* Shreb). Dose rate to the meristematic tissue initiation zones was both measured with thermoluminescent dosimeters and calculated from tissue radioactivity concentration. Dose rate estimates are summarized in Table 6.1 for mid-summer periods over two years (1969 and 1970) of observation. Total exposure for selected intervals can be integrated for desired time periods by assuming a linear decrease in dose rate (a plot showed slight curvilinearity with a negative slope).

Average seed production was reduced by 50% in the field radiation regime (Fig. 6.1) and it ranged from 17 to 9 rads/day during the first (1969) reproductive period. At the conclusion of the second season (1970) when dose rate had diminished by an additional 40%, seed production was 20% less than that of controls. Estimated cumulative exposure in the three-month period prior to flowering (during the time of probable floral initiation) was 1000 and 50 rads for 1969 and 1970, respectively. Short-term cumulative dose to primordial reproductive tissue was considered more realistic and probably more effective than total cumulative

dose from long-term (one and two year) exposures because continuous turnover and replacement of plant structures (leaf, stem, tiller) characterizes the growth pattern of grasses. In such a succession of tissues, each generation would receive a finite exposure and would be exposed to less than the cumulative dose. Derivative cells, however, may be affected by long-term exposures because their genetic apparatus may persist for several cell generations. Results indicated that seed production was affected by dose rate rather than total long-term exposure to a chronic in situ radiation source. Percentage reduction in the number of seeds per panicle was roughly half as much in 1969 as in 1970 (20 vs 50%), and it roughly corresponded to reduction in dose rate (<17 vs <9 rads/day) during periods of floral initiation.

Table 6.1 Comparison of dose rate ($R_{\beta} + R_{\gamma}$) to meristematic tissue^a receiving radiation exposure from external fallout and absorbed radioactivity

Date	Gamma and beta dose rate (rads/day)		
	External source	Internal source ^b	Total
August 1968	12 ^c	4.6	17
June 1969	9 ^d	0.5	9.5
July 1970	6 ^c	0.0	6

^aMeristem assumed to be 1 cm above soil surface, and possessed 0.5-cm-diam X 1.0-cm-long average dimensions.

^bDose rate calculations based on formulas from G. J. Hine and G. L. Brownell, *Radiation Dosimetry*, Academic, 1956; W. W. Pamley et al., p. 437 in *Some Aspects of Internal Irradiation*, T. F. Dougherty et al. (eds.), Pergamon, 1962; and L. O. Marinelli et al., *Am. J. Roentgenol.* 59, 260 (1948).

^cMeasured dose rate.

^dInterpolated dose rate.

1. NSF-URP.
2. Dual capacity.

Fig. 6.1. Average number of germinable and nongerminable seeds per panicle in experimental plots, 1969 and 1970. Sterilized and empty seeds were lumped as one category in 1969. No seeds germinated in control P₄ in 1970.

Percentage germination of irradiated seeds was only eight units less than that of controls in 1969 (Fig. 6.1), but this difference was not significant according to ANOVA tests. Results for the 1970 collection were inconclusive because all 23,781 seeds from one control plot failed to germinate. The factor which caused this failure has not been determined, but it is not likely that complete germination inhibition is a natural phenomenon in tall fescue seed. Normal seed production was observed for collections from this plot in 1969, and the anomaly in 1970 was attributed to undefined germination conditions in the laboratory. The germination failure necessitated the use of an estimated value in the ANOVA tests, consequently there was no significant difference between irradiated and control treatments in 1970. Results for both production and germination disclosed that the latter was a less sensitive indicator of radiation effects than seed production. This can be explained by considering developmental sequences of sexual reproduction in angiosperms (including grass), where deleterious effects for each genome probably would not be transferred to subsequent reproductive events (i.e., anomalies at sporogenesis may vanish before the onset of fertilization). The anomaly would disappear from the genome and population, and it would not be detected when scoring for effects at later stages of germinule development.

Another independent experiment which involved cotton rats was in progress in the experimental plots during vernal vegetative growth, floral initiation, and panicle collection in 1969. Appreciable disturbance to vegetation by the cotton rats required special statistical treatment of the seed production and germination results. Cotton rat grazing reduced seed production (Fig. 6.1) through direct but apparently subtle damage to the developing inflorescence. Relative to controls, the effect of grazing on seed production was significant in 1969 at the 5% level and in 1970 at the 1% level. The cotton rats were removed from the experimental areas in 1970, and suppression of production and germination in the second year apparently was a carryover effect from prior grazing impacts.

Results from this study indicate that a dose rate of 9 to 17 rads/day caused detectable effects on fescue reproduction. However, the effects were demonstrable only when intensive sampling procedures and sensitive statistical analyses were employed. When compared with laboratory exposure data for approximately equivalent doses to meadow fescue,³ the ORNL results indicate a factor of 10^3 reduction in the dose rates

3. A. H. Sparrow et al., in *Symposium on Survival of Food Crops and Livestock in the Event of Nuclear War*, BNL, Sept. 18, 1970 (in press).

which will produce an effect on grass. This occurred when the radioactivity was intimately associated with the organism's reproductive tissue and under field environmental conditions. Decreased seed production of pasture or forage grass may not be a serious consequence of contamination in an actual fallout situation because grasses are maximized for vegetative rather than seed yield. But if the same effect applies to cereal crops, and it probably would apply because wheat and corn are more radiosensitive than forage grass, then 50% reduction in grain yield could be expected if developing floral tissues were exposed to close-in nuclear fallout. Similar 50% decreases in seed production in native plant populations would greatly affect a species' reproductive capacity in terms of reduced ecesis and establishment. Resultant ecological manifestations would be lowered species success and changes in community composition, both of which would be indirect impacts attributable to sublethal deposits of fallout radiation.

EFFECTS OF FAST NEUTRON RADIATION ON WATER UPTAKE AND LOSS IN SUNFLOWER PLANTS

J. P. Witherspoon Linda Crouse

Plants exposed to sublethal doses of radiation often undergo morphological changes. These changes affect the response of the plant to environmental variables such as light and moisture. The purpose of this experiment was to determine the degree to which radiation-induced aberrant foliage affects moisture gains and losses from plants.

Saturation deficit is one measurement which can be used to express the water balance of a plant. It is defined as the water content of a plant part relative to the content if the plant were fully hydrated. This definition assumes that maximum growth occurs when the plant is fully hydrated. Saturation deficits exist where water loss exceeds water gain.

Potted sunflower plants (*Helianthus annuus*) were irradiated in the two-leaf stage at the Health Physics Research Reactor. Thirty plants each were exposed to 200, 400, and 800 rads (tissue dose in air) of fast neutron radiation (av energy 1 MeV). Exposure time was 18 min.

Following irradiation, plants were maintained in the greenhouse (71 to 81°F) in plastic pots containing silt-loam soil. One-half of the plants were maintained under moisture stress (50 ml of H₂O per pot twice weekly), and the other half was provided with adequate moisture (100 ml per pot twice weekly).

Weekly data were collected for five weeks on foliage saturation deficit, root and shoot weight, plant height, and leaf area. Saturation deficits were determined by placing cut shoots in a 100% humidity chamber for 24 hr to saturate the foliage. Then the expression

$$\frac{\text{saturated wt} - \text{fresh wt}}{\text{saturated wt} - \text{dry wt}} \times 100$$

was used to calculate saturation deficit. Leaf areas were determined by planimeter measurements of leaf imprints exposed on photosensitive Xerox paper.

Analyses of variance of height, weight, and leaf area data showed both moisture and dose treatments to be highly significant.

Figures 6.2 and 6.3 show saturation deficits expressed per cm² of leaf area as a function of both time and dose. In both plants receiving adequate moisture (Fig. 6.2) and those under moisture stress (Fig. 6.3), the foliage saturation deficits are essentially doubled following the 200-rad treatment and are more than doubled following the 400-rad treatment. No normal foliage developed following either the 200- or 400-rad treatment.

Nonirradiated controls (both moisture treatments) showed an increase in saturation deficit up to three weeks followed by a decrease up to five weeks (time of flowering). This increase probably was due to rapid vegetative growth previous to floral initiation when growth is inhibited. This pattern also occurred in all treatments except the 400-rad, adequate moisture, group.

As in the case of radiation treatments, the effect of the moisture stress treatments was essentially to double saturation deficits over those observed for adequate moisture treatments. It could be concluded that a 200-rad treatment had the same effect on moisture balance of the plant as halving the amount of water given to the plants. Thus the ability of these plants to absorb moisture at a rate commensurate with water losses through evapotranspiration is severely reduced by sublethal radiation levels which are sufficient to alter foliage structure. Increasing moisture stress proportionally increases this imbalance.

EFFECTS OF RADIATION ON ANIMAL POPULATIONS

Research on the effects of radiation on animal populations is not included in this report because of preparation of environmental impact statements for the Atomic Energy Commission. We are currently investi-

ORNL-DWG 72-434

Fig. 6.2. Saturation deficits in foliage of potted sunflower plants exposed to fast neutron radiation and maintained on 200 ml of water per week.

ORNL-DWG 72-435

Fig. 6.3. Saturation deficits in foliage of potted sunflower plants exposed to fast neutron radiation and maintained on 100 ml of water per week.

gating the effects of acute ^{60}Co gamma radiations on several animal populations while utilizing several different biological end points to assess the radiation effect. These studies include:

1. The determination of the rate of excretion of injected ($1\ \mu\text{Ci}$) ^{60}Co following an acute irradiation dose of 700 rads to a field-trapped population of pine mice, *Microtus pinetorum*, maintained in the laboratory;
2. The effect of an acute dose of 950 rads on the reproductive potential of a white-footed mouse *Peromyscus leucopus*, population;
3. The effect of a variable dose rate at 5000 rads total dose on the survivorship of a brown cricket, *Acheta domesticus*, population;
4. The influence of both gamma radiation and temperature on the excretion of ingested ^{137}Cs in brown crickets;
5. The development of a radiation profile for the migratory grasshopper, *Melanoplus sanguinipes*.

7. Effects of Radiation on Aquatic Systems

C. P. Allen G. E. Cosgrove²
B. G. Blaylock¹ M. Frank¹
N. A. Griffith¹

The scientific staff is fully committed to the preparation of environmental impact statements for the Atomic Energy Commission; therefore, the formal annual report was not prepared. Research that was completed and some that is continuing at a reduced rate is summarized briefly.

1. Population and cytogenetic studies: Ten years or approximately 50 generations after the first sample was analyzed the salivary gland chromosomes of 247 *Chironomus tentans* larvae from White Oak Creek were analyzed for chromosome aberrations. No radiation-induced aberrations were detected in the samples. The dose rate from the bottom sediments had decreased from 230 rads/year in 1960 to 11 rads/year in 1970. An additional 400 larvae were collected and are being analyzed to continue our long-term study of a natural population exposed to higher-than-background levels of radiation. (Blaylock and Allen)

2. Chromosome aberrations produced by tritiated water: A dose-response curve for the production of chromosome aberrations in *Chironomus riparius* cultured in tritiated water was prepared. The lowest concentration at which aberrations were detected was 125 $\mu\text{Ci/ml}$ (~ 765 rads). The relative biological effectiveness for beta radiation from incorporated tritium was approximately one. Additional data are being collected at concentrations of tritiated water less than 125 $\mu\text{Ci/ml}$. (Blaylock and Allen)

3. Hatchability of carp (*Cyprinus carpio*) eggs in different concentrations of tritiated water: Carp eggs spawned in different concentrations of tritiated water ranging from 50 to 1000 $\mu\text{Ci/ml}$ showed no significant difference from the controls in the percentage of eggs that hatched. Indications were that a higher mortality

rate occurred in the newly hatched fish from the higher concentrations of tritiated water. The biological half-life of tritium in these newly hatched fish was 6.5 days. (Blaylock, Griffith, and Allen)

4. Synergistic effect of pesticides and radiation: The effects of DDT, 2-4-5 T, and radiation on the hatchability of carp eggs were tested previously. When either DDT or 2-4-5 T was tested in combination with acute irradiation, a synergistic effect was detected. (Blaylock and Allen)

5. Effect of acute ionizing radiation on carp (*Cyprinus carpio*) embryos: Changes in development and hatchability of carp embryos showed radiosensitivity decreased as development increased after organogenesis. Stages in decreasing order of sensitivity were newly fertilized eggs, early gastrulation, early cleavage, and postorganogenesis. In general the earlier the stage of development the more severe the effect of radiation on embryo development and hatchability. (Frank)

6. Effect of temperature and irradiation on *Gambusia*: Mortality and histological investigations were conducted on the mosquito fish (*Gambusia affinis affinis*), which were exposed to acute and chronic radiation and maintained at 15 and 25°C. In the chronic irradiation experiment a difference of 10°C did not produce a detectable difference in the mortality of *Gambusia* or in radiation damage to the different tissue. In the acute studies mortalities occurred faster at 25 than at 15°C, but changes in hemopoietic organs and ovaries were more severe at 15°C. (Blaylock, Cosgrove, and Allen)

1. Dual capacity.
2. Biology Division.

8. Radionuclide Cycling in Aquatic Systems

M. Carter ²	N. A. Griffith ¹
E. B. Douple ³	H. Hackett ²
J. W. Elwood ¹	D. J. Nelson ¹
M. Frank ¹	G. U. Ulrikson ¹

The annual report was not prepared this year because the scientific staff is fully committed to the preparation of environmental impact statements for the Atomic Energy Commission.

However, some research was completed and some is continuing at a reduced rate. Topics on which we have data include:

1. The biological half-life of ^{137}Cs and ^{60}Co in turtles from White Oak Lake.
2. A further analysis of the interacting effects of temperature, feeding rates, growth rates, and the turnover of ^{137}Cs by bluegills.
3. Studies of the uptake and turnover of tritium in White Oak Lake in bluegills as well as data which show that the concentration factor of ^3H in chronically exposed fish is approximately one.
4. Additional research on ^3H in *Gambusia* from White Oak Lake showed that the concentration of ^3H in fish approximated that of the water. When the ambient concentrations vary, the concentrations in fish also vary because of the rapid turnover of body water and a high proportion of the hydrogen in fish is in body water.
5. White Oak Lake was sampled intensively to obtain a more complete knowledge of the distribution of radionuclides in various components of the food chain.

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1. Dual capacity.
 2. NSF-URP.
 3. AEC-Health Physics Fellow.

9. Thermal Effects Studies

P. Adamus ¹	C. C. Coutant	C. F. Goodyear	J. M. P. McNelle ³
S. H. Bowen ²	M. A. Eischen ²	H. Guderley ²	W. G. Stockdale ⁴
D. S. Carroll	J. W. Gooch	P. E. Neuman	G. U. Ulrikson ⁵

Because of compelling activities associated with the preparation of environmental impact statements, the formal annual report was not prepared. Research that was completed or is under way is summarized briefly for each project.

1. Temperature tolerance of the Asiatic clam, *Corbicula manilensis*: The time-temperature conditions for the death of this clam have been determined in the laboratory for populations acclimated to a range of holding temperatures. (Coutant)

2. The evaluation of effects of thermal stress on fish by means of electrophoretic separations of blood serum proteins: There were changes in blood serum proteins of juvenile rainbow trout that were given various timed exposures to potentially lethal temperatures. (Ulrikson and Guderley)

3. Temperature selection in the field by largemouth bass tagged with an ultrasonic, temperature-sensing fish tag: An ultrasonic fish tag was developed for monitoring temperatures selected by fish in the field. Several largemouth bass have been tracked in the vicinity of TVA's Bull Run Steam Plant near Oak Ridge. (Coutant and Rochelle)

4. Responses of Clinch River fishes to shutdown and startup of Bull Run Steam Plant in spring 1971: Fish that were attracted to the warm water discharge of the plant in each spring dispersed when the heat ceased, although water flow was maintained for several hours by pumping unheated water. The fish did not return when pumps alone were started several days later, but returned only after the cooling water was heated. (Coutant)

5. Annual review of thermal effects literature: Literature of 1970 on thermal effects was reviewed, the review published in the *Journal of the Water Pollution Control Federation*, and the bibliographic information stored in the computer files of the Nuclear Safety

Information System and the Ecological Sciences Information System. (Coutant)

6. Temperature effect on feeding competition between bluegill and rainbow trout: Acclimation temperature affected the outcome of feeding competition, with equal feeding success occurring at 22.5°C. Trout were progressively more successful at colder temperatures, and bluegill at the higher temperatures. (Bowen and Coutant)

7. Temperature effect on relative susceptibility of juvenile largemouth bass and juvenile goldfish to predation: No clear trend in thermal effects was identified in preliminary testing over a range of acclimation temperatures, although selection was consistently shown at several of the temperatures. (Coutant)

8. Survey of current thermal effects research: An inventory of ongoing (1970) thermal effects research was developed and published. (Ulrikson and Stockdale)

9. Zooplankton studies at Bull Run Steam Plant: Zooplankton collections were made in the summers of 1970 and 1971. Some reduction of zooplankton in passing through the plant was identified, although analyses of samples are incomplete. (Adamus and Coutant)

10. Experimental marking of nonsalmonids with liquid nitrogen cold brand: The cold-branding technique, heretofore shown to be suitable only for salmonids, was used successfully on bluegill, sauger, red horse, and largemouth bass. (Coutant)

11. Temperature effect on growth of bluegill: Bluegill growth rates were affected by acclimation temperature. (Bowen)

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1. ORAU participant.
 2. Great Lakes Colleges Association.
 3. Instrumentation and Controls Division.
 4. Reactor Division.
 5. Dual capacity.

10. Ecological Sciences Information Center

C. Oen B. N. Collier G. U. Ulrikson

The Ecological Sciences Information Center (ESIC), because of the increased work load experienced in serving the Oak Ridge National Laboratory Environmental Impact Statement Committee, has not prepared a formal annual report. The mission of ESIC is to

collect, analyze, and store in machine-readable form ecological bibliographic references, and make these computerized files of information available to the Ecological Sciences Division, the AEC, and other interested groups.

11. Other Programs

A. APPLICATIONS MODELING

R. V. O'Neill

O. W. Burke¹

Duane Chapman²

R. E. Funderlic³

M. T. Heath³

Joan M. Hett

J. B. Mankin³

Mark Reeves III³

Another Divisional activity involves the application of modeling to the solution of environmental problems. In this type of research it is essential that the problem be rigorously defined, and the model will have to contain the modifications, simplifications, and assumptions appropriate to the problem. The underlying basic models are derived from various ecological process models developed in other Divisional programs. These small exercises in applications modeling serve to provide further insight into the design of ecosystem models. Additionally it serves to relate the more basic studies in systems modeling to the immediate and pressing problems associated with the impact of technology on the environment.

ECOLOGY AND RESOURCE ECONOMICS: AN ATTEMPT AT INTEGRATION

D. Chapman R. V. O'Neill

Solution of complex environmental problems requires the application of expertise from a wide range of traditional disciplines. The difficulties in integrating these disciplines often are proportional to the difference in subject matter and methodologies. A recent report⁴ considered the problems of integrating economic and ecological theory as an aid to finding a more

satisfactory relationship between man and his environment.

Effective application of a social science – economics, together with a natural science – ecology, requires the establishment of a logical basis for integration. Such a basis can be found in the concept of functional systems analysis. The state of a functional system at any point in time can be defined in terms of the current values of a set of variables. Variables might be costs and values in the economic system or population numbers in the ecological system. Interactions between economic and ecological functional systems can be treated in a precise manner by specifying processes or functions which relate variables in one system to variables in the other systems. With the definition of appropriate interaction processes, a new functional system can be defined as the union of an economic and an ecological system.

A preliminary application of the approach can be seen from an analysis of the conflict between demands for increased power production and demands for greater environmental quality. A rapidly expanding population, combined with technological advances such as television, electric heating, and air conditioning, creates a demand for increased power generation (Fig. 11.1). Although this trend may be accompanied by increasing market costs, supply demand equilibria seem to be characterized by increasing power generation, especially when government subsidies are considered. But as detrimental environmental changes become increasingly apparent to society, the public begins to perceive effects on human values such as health and esthetics. The result is a strong negative feedback which militates

1. Instrumentation and Controls Division.

2. ORNL-NSF IRRPOS Program.

3. Mathematics Division.

4. D. Chapman and R. V. O'Neill, ORNL-4641 (1970).

Fig. 11.1. Power system schema: feedbacks influencing new plant construction. Plus sign denotes positive influence and minus sign denotes negative influence.

Fig. 11.2. Market and social equilibria. Vertical axis represents power costs and horizontal axis represents per capita power production.

C_m = Market cost function	C_s = Marginal social cost function
P_m = Market demand function	V_s = Marginal social demand function
C_{me} = Market equilibrium cost	C_{se} = Social equilibrium cost
P_{me} = Market equilibrium price	V_{se} = Social equilibrium marginal value
C_{sa} = Cost of actual supply	P_{ma} = Price of actual supply
X_{me} = Market equilibrium output	X_{se} = Social equilibrium output
X_{ad} = Output demand at price P_{ma}	X_{as} = Output actually supplied

against new power facilities. As education increases public awareness, this negative feedback is intensified. A dynamic social, technical, and economic system has evolved which may or may not approach equilibrium in time and space.

The concept of functional systems analysis can be applied to a specific example of the power dilemma, "blackouts" or "brownouts" in major cities (Fig. 11.2). At a given point in time, the intersection of the market supply and demand functions defines the market equilibrium as X_{me} with price P_{me} . But environmental effects of power generation, as perceived by society, cause a different social equilibrium X_{se} , defined by the intersection of the marginal social cost and marginal social value functions. The differences in equilibria create conflict as power companies attempt to build more plants and conservation-minded citizens attempt to prevent construction. The total power production from plants actually built is some compromise X_{as} . At actual output X_{as} , the utility incurs market cost C_{ma} . The regulatory agency requires the utility to set its market price P_{ma} at or near C_{ma} . With price P_{ma} the public, acting as consumers, demands quantity X_{ad} . This quantity is substantially in excess of X_{as} , the amount actually supplied. The theory then predicts a demand in excess of supply resulting in "brownouts."

Although current attempts to integrate economic and ecological theory have been of a preliminary nature, the success of the interaction in providing a reasoned explanation for one aspect of the power dilemma

suggests the usefulness of continued developments in this direction.

SYSTEMS ANALYSIS OF THE ALEUT ECOSYSTEM

J. M. Hett R. V. O'Neill

The benefits of applying systems analytic techniques at an early stage of research are examined by developing and analyzing a preliminary model for the Aleutian ecosystem. The Aleut population is considered as consumer in the total cycling of carbon. Prior to first contact with civilization, the population was intimately dependent on the physical and biological environment for shelter, clothing, and food. As a marine hunting and gathering people, the Aleuts depended on the ocean to provide a major portion of their food while the terrestrial system provided various supplements.

The carbon cycle model and data (Fig. 11.3) are crude as is appropriate at this preliminary stage of knowledge. Man is emphasized as a consumer, the top of a natural food chain. The state variables were chosen to include components most utilized by man and major variables involved in cycling carbon through these components. The amount of carbon in each state variable (excluding man) was obtained by multiplying average world figures⁵ by 2.5×10^{-4} , the approximate percentage of the world's surface occupied by the Aleut

5. B. Bolin, *Sci. Amer.* 233(3), 125-32 (1970).

Fig. 11.3. Carbon model for the Aleutian ecosystem. The values in each compartment represent metric tons (10^3) of carbon at steady state. Numbers on the arrows represent the flux of carbon (metric tons/year) between compartments.

domain. The amount of carbon in the human population was approximated by subdividing into age classes and supplying a mean weight.

Analyses of the model (discussed in the following section) indicate the need for extensive research on the marine food supply and offer hypotheses for the dependence of Aleuts on the sea. Conclusions of this study can be summarized as follows:

1. Problems of interest to anthropologists can be feasibly approached by applying environmental systems analysis;
2. Despite the simplicity of the model, the analyses revealed that the model faithfully reflected the general nature of the system and confirmed prior intuitions about the dependence on a marine food supply and the relative stability of the marine system;
3. At the same time, the analyses indicated sensitivities to the marine system far in excess of our intuition;
4. The Aleut population, as a consumer in a natural system, played a relatively minor role in maintaining or affecting the stability of the ecosystem as defined by the rate of recovery from disturbance;
5. Perhaps the most interesting conclusion to be reached from this study is the benefit which can be derived from the early application of systems analysis in research projects on complex ecosystems.

SENSITIVITY ANALYSIS OF AN ALEUTIAN ECOSYSTEM

R. E. Funderlic M. T. Heath

Ecological Sciences Division personnel have developed a simple 9×9 linear compartmental model of the Aleutian ecosystem (see previous system). The model can be expressed as a system of differential equations $\dot{x} = Ax$, where $A = (a_{jk})$ is the matrix of transfer coefficients and x is the vector of concentrations in the compartments. The vectors $\partial x(\infty)/\partial a_{jk}$ are helpful in gaining insight into why the Aleut population has evolved such an intimate dependence on the marine subsystem. For this model the matrix A is irreducible, and therefore $Ax(\infty) = \dot{x}(\infty) = 0$ has only one solution, $x(\infty)$, up to a scalar multiple.⁶ Thus, the normalization $\sum x_k(\infty) = 1$ determines $x(\infty)$ uniquely.

Small changes in the matrix A do not change the rank = 8 of A since the sum of the row vectors is the zero

vector. Thus $x(\infty)$ is a continuous and rational function of the elements of A . This proves the existence of $\partial x(\infty)/\partial a_{jk}$. Therefore $\partial [Ax(\infty)]/\partial a_{jk} = A [\partial x(\infty)/\partial a_{jk}] + x_k(\infty)(e_j - e_k)$, where all the components of the vector e_i are 0 except the i th which is 1. Thus $z \equiv \partial x(\infty)/\partial a_{jk}$ satisfies

$$Az = x_k(\infty)(e_j - e_k). \quad (1)$$

The solutions of (1) are of the form $z + cx(\infty)$, where z is any particular solution of (1) and c is any scalar. A multiple of the vector $\partial x(\infty)/\partial a_{jk}$ may be determined from (1) and $\sum \partial x_k(\infty)/\partial a_{jk} = 0$.

With respect to the Aleut model, calculations based on the above derivation show that land plants are about 300 times more sensitive to a change in uptake of atmospheric carbon than marine animals are to changes in uptake of surface water carbon. This would tend to indicate that the marine subsystem is a more reliable food source and might explain the dependence of the population on it.

A SIMPLE MODEL FOR DDT AND DDE MOVEMENT IN HUMAN FOOD CHAINS

R. V. O'Neill O. W. Burke

At the request of the DDT Advisory Committee, Environmental Protection Agency, a simple model was developed for DDT and DDE movement in food chains leading to man. The objective was to estimate future concentrations in human tissues under various assumptions about DDT application.

The model, which was limited to the data supplied by the Committee, consisted of three differential equations. The first two equations expressed the time behavior of concentrations in food contaminated by direct spraying and in food contaminated by uptake from an environmental pool. The third equation treated concentrations in human adipose tissue. The model was implemented on an analog computer (Fig. 11.4), and coefficients were chosen to match the available DDT data as faithfully as possible. The model forecasted a continued reduction in DDT and DDE concentrations as long as DDT usage continues to decline (Table 11.1), or at least does not increase above the 1972 level. Cases 1, 3, and 5 showed that the system is dominated by an environmental pool with slow turnover. Therefore, concentrations in man can be expected to decrease very slowly and over a considerable period of time. Decreasing DDT usage more rapidly, or stopping application in 1972 (a year earlier than expected), should

6. R. E. Funderlic and M. T. Heath, ORNL-IBP-71-4 (August 1971).

ORNL-DWG 71-0982

Fig. 11.4. Analog computer program for DDT and DDE food chain model. In the program, circles indicate potentiometers which correspond to model parameters. Integrators are indicated by a triangle with attached rectangle and correspond to state variables. Triangles indicate amplifiers which serve to sum or change the sign of quantities.

Table 11.1. DDT + DDE concentrations in human adipose tissue (ppm) predicted by the model with various assumptions about DDT usage

Year	1 Usage reduced at present rate	2 Usage maintained at 1966 levels	3 Usage reduced at twice present rate	4 Usage maintained at 1972 level (5×10^6 lb)	5 Usage stopped in 1972	6 Restrictions lifted in 1972, usage resumes at level 1966
1970	5.14	5.30	4.98	5.14	5.14	5.14
1974	4.18	5.08	3.75	4.20	4.18	4.43
1978	3.41	5.32	3.00	3.53	3.40	4.82
1982	2.78	5.60	2.44	3.02	2.78	5.35
1986	2.27	5.84	1.99	2.60	2.27	5.82
1990	1.86	6.03	1.62	2.25	1.85	6.21
1994	1.52	6.20	1.33	1.98	1.51	6.52
1998	1.24	6.32	1.08	1.75	1.23	6.78
2002	1.01	6.42	0.88	1.56	1.01	7.00
2006	0.82	6.52	0.72	1.41	0.82	7.17
2010	0.67	6.56	0.58	1.29	0.67	7.31
2014	0.55	6.65	0.48	1.18	0.55	7.42
2018	0.45	6.70	0.39	1.10	0.45	7.52
2022	0.37	6.73	0.32	1.03	0.37	7.60

Fig. 11.5. Sulfur dioxide concentrations in air and potential effects on plant crops resulting from the construction of a hypothetical coal-burning power plant. The results are based on a Gaussian plume air diffusion model and information on SO₂ effects taken from the literature. The total area depicted represents a hypothetical county in the southeastern United States.

have little effect on concentrations in the next century. However, if DDT usage is permitted to increase toward the high 1966 level, concentrations in man could be expected to increase. A slow increase would continue for a considerable period, and concentrations would be significantly above present levels in the next century.

REGIONAL ECOLOGICAL EFFECTS OF A HYPOTHETICAL POWER PLANT

R. V. O'Neill M. Reeves III J. B. Mankin

A modeling study on the ecological effects of power plant siting has been conducted in cooperation with the Regional Modeling Study, ORNL-NSF Environmental Program. In addressing the problems, various portions of a preliminary regional model⁷ were applied with crude estimates supplied where particular submodels had not been completely developed. The size of the hypothetical power plant and its location were es-

timated from socioeconomic and land-use simulation portions of the preliminary model.

A Gaussian plume air diffusion model was used to predict concentrations of SO₂ and flyash as grid point: across the region. Information from the ecological literature was used to predict damage to commercial plants in the area (Fig. 11.5). Reduced productivity in abandoned field ecosystems, located at various distances from the plant site, was predicted as a result of shading effects from suspended flyash.

Results indicated that most effects were highly localized but that damage to sensitive plants, such as alfalfa, might extend for distances of perhaps ten miles downwind. The total exercise provided valuable insight into the applicability of ecological information in addressing environmental problems.

7. V. R. Cain, ORNL-NSF Environmental Program, ORNL (in press).

B. APPLICATIONS RESEARCH

B. G. Blaylock ⁸	M. S. Hibbs ^{1 5}	R. Roberts ^{1 2}
R. C. Dahlman ^{8, 9}	J. W. Huckabec ^{1 2}	Y. A. Tanaka ^{1 3}
M. Davis ^{1 0}	L. K. Mann ⁸	A. Watson ^{1 4}
R. Gaskins ^{1 1}	R. Mowbray ^{1 3}	J. P. Witherspoon ⁸
N. A. Griffith ⁸	D. E. Reichle ⁸	M. Witkamp ⁸

Special research studies and analyses are valuable sources of new ideas for program development. In addition, they provide useful information and data dealing with current environmental problems, many of which are indirectly related to the total energy problem, although they may fall outside the scope of existing projects. Some studies involve lead-time research by summer participants; others involve student assignees working under senior research staff members. These kinds of efforts help to maintain the vitality of the Division research program and lead to new perspectives in application of research to societal problems.

CYCLING OF HEAVY METALS

J. P. Witherspoon

M. Davis R. Roberts
R. Gaskins G. Stein
M. Witkamp

Lead-time research was initiated on the cycling of heavy metals in terrestrial and aquatic microcosms. This work is currently supported by the IRRPOS heavy metal studies project to develop techniques which will be useful in evaluating the behavior of heavy metals in ecological systems. Cadmium-115 was introduced into two large (6 X 9 X 17 dm) microcosms. Each microcosm contained both terrestrial and aquatic components. Cadmium ($^{115}\text{CdCl}_2$) was applied to the terrestrial portion in the form of a simulated rain of 1 liter volume containing 284 μCi of ^{115}Cd . Subsequently, two cadmium-free simulated rains per week (total of 2.5 cm) were applied. Litter, soil, water, sediment, and biotic components were sampled for a period of 21 days following application of Cd.

Rates of movement and bioaccumulation of ^{115}Cd between microcosm components were determined for 21 days following application (Table 11.2). Results showed that ^{115m}Cd is accumulated slowly in plants, particularly when the plants must compete with soil or other organic matter for the Cd ions. Loss of the cadmium from the terrestrial to the aquatic system did occur, but was moderated greatly by the apparent unavailability of soil-bound Cd to soil solution and plant uptake. The long-term fate of a soil saturated with cadmium is unknown. Cadmium was leached to the aquatic portions and accumulated in sediments more rapidly than any living organism; fish were shown to assimilate cadmium from food more slowly than snails.

Further experiments were designed to elucidate the roles of organic and inorganic substrates and microbiota in the retention of cadmium in both terrestrial and aquatic microcosms. Retention of Cd added in simulated rain (2.5 cm/week) to terrestrial microcosms with leaf litter or soil was 98.5 and 99.5%, respectively. An additional 5 cm of Cd-free simulated rain leached less than 2.5% of the absorbed Cd from the sediments. These results verify the immobility of Cd in terrestrial substrates. Total percentage of Cd retained by the soil substrate was not affected by microbiota, although the distribution of Cd in the soil profile was modified. Microbiota in the top 2.4 mm contained 32% of the added Cd while the inorganic fraction contained 56%.

In aquatic microcosms with organic sediments, 2% of the added Cd remained in the water while 92% was absorbed by the sediment and 6% was taken up by microbes. Corresponding data for aquatic microcosms with inorganic sediment were: 1% in water, 96% in sediment, and 3% in biota. As in the terrestrial microcosms, surface microbiota immobilized 20% of total Cd in the top 2.5 cm of the inorganic sediment, and reduced Cd diffusion into deeper layers. These experiments indicate that organic substrates retain less Cd than inorganic substrate. Microbiota did not significantly increase retention by terrestrial substrates but did increase absorption by aquatic sediments. In both systems, surface microbiota reduced diffusion into deeper sediment layers.

Comparative studies were initiated on the uptake of ^{115}Cd and ^{65}Zn from soil by plants which indicated

8. Dual capacity.

9. Federal Repository Project.

10. ORAU undergraduate participant.

11. ORAU-ESD undergraduate participant, Emory University.

12. ORNL-NSF IRRPOS Program.

13. Consultant, University of Tennessee.

14. AEC Predoctoral Fellow.

15. NSF-URP.

Table 11.2. Distribution of ^{115m}Cd in components of microcosms 21 days after application of $284\ \mu\text{Ci}$ to the terrestrial subsystem in a simulated rain

Microcosm component	Average percent of total inoculum of $^{115m}\text{Cd} \pm \text{S.E.}$
Terrestrial	
Mosses	9.03 ± 1.45
Higher plants	0.20 ± 0.08
Litter	12.96 ± 2.91
Soil	72.45 ± 5.41
	<u>94.64</u>
Aquatic	
Water	0.19 ± 0.008
Fish	0.0004 ± 0.0001
Snails	0.06 ± 0.02
Watercress	0.04 ± 0.003
Sediment	3.14 ± 0.01
	<u>3.43</u>
Container surface	1.93

that Cd is preferentially accumulated over Zn. Bean plants grown on silt-loam soil treated with $^{115}\text{CdCl}_2$ and $^{65}\text{ZnCl}_2$ solutions after five weeks showed Cd/Zn ratios of 1.3 and 2.9 in foliage and roots, respectively. Neither heavy metal was concentrated by plant tissues; plant-to-soil concentration ratios ranged between 0.25 and 0.33. Mobility of both metals in the soil was slight; after five weeks and 23 cm of rain, >90% of both elements remained in the top 7.6 cm of soil.

BEHAVIOR OF METHYLMERCURY AND MERCURIC NITRATE IN NATURAL STREAM ECOSYSTEMS¹⁶

J. W. Huckabee B. G. Blaylock
N. A. Griffith

Concentrations of mercury compounds occur in many natural waters in North America, Europe, and Asia. In some cases mercury poisoning to humans or the biota has resulted. Methylmercury is the most toxic mercurial to vertebrates, and inorganic mercurials are methylated by microorganisms present in sediments. Although discharge of mercurials to the environment has diminished, large quantities of persistent mercury remain in stream and lake sediments. Knowledge of the comparative behavior of mercury compounds in natural waters, such as retention time of mercurials in a body of water and food chains, is important for assessing the potential environmental hazard associated with these compounds.

We tagged one small oligotrophic stream within the AEC-ORNL Reservation with radioactive $\text{CH}_3^{203}\text{HgCl}$ and a similar stream with $^{197}\text{Hg}(\text{NO}_3)_2$ to determine the movement and transfer of these two mercury compounds within natural stream ecosystems.

The study sections of the streams were 100 m long measured downstream from the point of isotope release with sampling stations at 10, 20, 40, 70, and 100 m. In addition, fish were collected 200 m downstream. The two streams used in the experiments are compared in Table 11.3.

The discharge of Walker Branch was measured at the two weirs of the Walker Branch watershed project located immediately upstream from this experimental area. A Parshall flume was installed in White Oak Creek to measure discharge for this experiment. The sediments of both creeks consist of subangular gravel-size rubble and poorly sorted sand. There is little organic detritus.

A 4-liter polyethylene bottle inverted into a funnel fitted with a Pasteur pipette was used to release the isotope into each stream. The duration of isotope release was arbitrary inasmuch as it was intended to represent an acute exposure. Release time was 11.8 min in White Oak Creek and 19.1 min in Walker Branch.

A fluorescein dye was added immediately before and after the isotope spike. Water samples were taken from the time the first dye appeared at a station until none of the postspike dye was visible, thus bracketing the isotope spike as it flowed past the sampling stations. The amount of isotope retained in each subsection of the stream and the concentration factor calculations were based on the disintegrations per minute of these water samples collected during flowthrough of the isotopes. Water samples were collected at 5-min intervals. Duration of sampling was 90 min at the lower stations due to dispersion of the isotopes.

Two different water sampling techniques were employed. Five milliliters of water was pipetted into a counting tube every 5 min, and 250 ml of water was collected in polyethylene bottles every 10 min. The latter were poured through a $0.45\text{-}\mu$ Millipore filter, and the filtered residue's gamma-ray activity was counted. A portable generator was used to power a pump for the filtering apparatus, and filtrations were accomplished as the samples were collected. This technique minimized the possibility of the mercury plating out on the sides of the bottles. Table 11.4 shows the percentage of the water's gamma-ray activity contained in the residue. The increase of this percentage for mercuric nitrate

16. Research sponsored by the National Science Foundation.

downstream indicates adsorption on particulate matter. The particles seem to have less affinity for methylmercury.

At 4 hr postspike collections were made at each sampling station of sediments, periphyton, aquatic macrophytes, snails, and fish. Fish and emergent plants were not present at every station. Collections were then made at regular intervals for 9 days in Walker Branch (^{197}Hg) and 49 days in White Oak Creek (^{203}Hg).

Snails and macrophytes were easily hand collected in the shallow water. Sediments were taken in a 1-cm-diam glass tube. Periphyton was sampled by taking three rocks at each collection per station and removing the growth in the lab. Fish were taken by means of a small battery-powered shocker.

Gamma-ray activity of the samples was measured by counting the 279-keV gamma rays of ^{203}Hg or the 77-keV gamma rays and x rays associated with ^{197}Hg . Activities are expressed as dpm/wt (wet weight), corrected for half-life and background. The samples were small enough to avoid self-shielding.

The variation in size of the fish (<0.1 to 10.0 g) caused some variation in count rate due to geometry, even though the sample was never over 1 in. deep in the counting tube. Simple tests using different-shaped

pieces of sponge saturated with known volumes of isotope showed that the maximum size difference encountered between two fish would cause an error smaller than statistical variation. In the $\text{Hg}(\text{NO}_3)_2$ and $\text{CH}_3^{203}\text{HgCl}$ experiments, 75.20 and 81.23% was retained in the first 100 m, respectively. Table 11.5 shows the percent retention of the isotope in each subsection of the study reach. The location of pools and riffles produced uneven flow rates in each stream subsection. The differing retention of the isotope for each subsection (Table 11.5) may be accounted for by this varying residence time of the isotope in each subsection.

The concentration factor of each ecosystem component sampled was calculated by

$$CF = \frac{\text{dpm/g sample}}{\text{dpm/ml subsection water}}$$

where dpm/ml subsection water is the percentage of the total activity entering the subsection. Concentration factors were calculated for each ecosystem component sampled. Figure 11.6 compares the concentration factors for these components in each stream at nine days postspike.

Table 11.3. Physical and experimental parameters of two streams at AEC-ORNL tagged with $\text{CH}_3^{203}\text{HgCl}$ and $^{197}\text{Hg}(\text{NO}_3)_2$

	White Oak Creek ($\text{CH}_3^{203}\text{HgCl}$) September 1, 1971, 0900 hr	Walker Branch [$^{197}\text{Hg}(\text{NO}_3)_2$] October 5, 1971, 1000 hr
Isotope added, mCi	1.65	4.48
Total Hg added, mg	0.32	19.73
Spike duration, min	11.8	19.1
pH	8.1	8.0
Temperature, °C	16.5	17.0
Discharge, liters/min	325.6	347.8
Dissolved O_2	Saturated	Saturated
Stable Hg concentration in stream water (ng/ml)	0.0144	0.0128

Table 11.4. Percentage of stream water activity contained on suspended particulates in mercury tag experiments

Reach	White Oak Creek ($\text{CH}_3^{203}\text{HgCl}$)	Walker Branch [$^{197}\text{Hg}(\text{NO}_3)_2$]
1	7	7
2	2	10
3	6	19
4	4	17
5	4	25

Table 11.5. Percentage retention of mercury in each stream subsection after tagging with $\text{CH}_3^{203}\text{HgCl}$ and $^{197}\text{Hg}(\text{NO}_3)_2$

Subsection	White Oak Creek ($\text{CH}_3^{203}\text{HgCl}$)	Walker Branch [$^{197}\text{Hg}(\text{NO}_3)_2$]
1	Not available	10.70
2	31.43	29.66
3	29.51	25.41
4	14.87	.23
5	5.42	9.20
Total after isotope flowthrough	81.23	75.20

Fish concentrate and retain methylmercury to a greater extent than other biota and inorganic sediments. During the course of the sample collecting, a few crayfish and salamanders were occasionally caught. The methylmercury concentrations in these species were always less than in fish from the same stream subsection. The difference in methylmercury concentrations in *Rhinichthys cataractae* (longnose dace) and *Campostoma anomalum* (stoneroller) could be due to the trophic level these species occupy. Gut content analysis showed that dace fed on a variety of small invertebrates while stonerollers fed on algae, which was mostly diatoms. However, dace also concentrated

$^{197}\text{Hg}(\text{NO}_3)_2$ more than *Cottus caroliniae* (Tennessee sculpin). In the methylmercury experiment, a few sculpins were occasionally taken, and always had a smaller mercury concentration factor than comparable dace. The gut contents of sculpins showed a higher percentage of macroinvertebrates than dace.

In contrast to methylmercury, the fish concentrate mercuric nitrate to a lesser extent than any of the other components sampled. Both isotopes were detectable in fish at 200 m (Table 11.6). At 60 days after the isotope release, 0.7 ppb of mercury was detected in dace and 0.5 ppb in stonerollers at approximately 300 m. At this point, White Oak Creek disappears underground in the tilted limestone strata. Five days after isotope release in Walker Branch, 0.25 ppb of mercury was detected in the snail (*Goniobasis clavaeformis*) at 500 m.

Mercury concentrations are expressed as ppb and dpm/mg at 200 m and below because no comparable water measurements were made at these points.

Fig. 11.6. Mercury concentration factors at nine days post-spike.

TOXICITY OF ORGANIC AND INORGANIC ARSENICALS

R. I. Van Hook

D. E. Reichle A. Watson

Arsenical formulations have come into large-scale production for use in thinning trees, defoliation of cotton, renovating turf, and as general postemergent weed-control agents. Little is known of the ultimate fate of these materials in the environment; even less is available concerning long- and short-term effects upon

Table 11.6. Mean mercury concentrations (ppb and dpm/g) in fish at 200 m in mercury tag stream experiments

Day	White Oak Creek ($\text{CH}_3 ^{203}\text{HgCl}$)				Walker Branch [$^{197}\text{Hg}(\text{NO}_3)_2$]			
	<i>R. cataractae</i>		<i>Campostoma anomalum</i>		<i>R. cataractae</i>		<i>Cottus caroliniae</i>	
	ppb	dpm/mg	ppb	dpm/mg	ppb	dpm/mg	ppb	dpm/mg
1					0.5	0.28	1.6	0.83
2					0.2	0.12	0.1	0.06
3					0.4	0.20		
5					0.9	0.47	0.1	0.06
7					0.5	0.27		
9					0.2	0.12		
16	1.7	19.91	0.3	3.58				
20	2.1	29.74	1.1	12.83				
28	1.5	16.07	0.7	7.84				
35	1.7	20.15						
42	0.8	8.87	1.2	14.81				
49	0.6	4.20	0.8	7.86

Fig. 11.7. Whole-body arsenic concentrations following a 14-day chronic ingestion of cacodylic acid (35% As), Phytar-560 (13% As), As_2O_5 (65% As), and As_2O_3 (76% As) expressed as a function of administered dose. Arrows indicate the LD_{50-14} .

nontarget organisms. One of the basic questions that has been unanswered is that of what are the actual concentrations of elemental arsenic in a population of organisms exposed to arsenical materials. As one of our lead-time studies for the Toxic Materials in the Environment Project, a population of meadow katydids, *Conocephalus*, was exposed to varying dosages of cacodylic acid, Phytar-560, arsenic pentoxide, and arsenic trioxide. Lethal dosages required to kill 50% of the population were determined at the end of 14 days. Whole-body concentrations of arsenic were determined by neutron activation analysis for those animals that died during the 14-day period.

Whole-body arsenic concentrations at 14 days post-treatment expressed as a function of dose are shown in Fig. 11.7 for cacodylic acid, Phytar-560, arsenic pentoxide, and arsenic trioxide, respectively. The arrow in each figure points to the maximum likelihood estimate of the dose required to kill 50% of the population in 14 days. Errors associated with whole-body arsenic determinations ranged from 5 to 10% of the means illustrated. Dosages required to kill 50% of the population in 14 days were higher for the organic arsenicals (cacodylic acid, 7.5 ppm and Phytar-560, 3.5 ppm) than for the inorganic arsenicals (arsenic pentoxide, 2.8 ppm and arsenic trioxide, 0.2 ppm). This indicates that the inorganic arsenicals are much more toxic to the grasshopper population than are the organic arsenicals with the trivalent form (arsenic trioxide) being the most toxic.

As indicated in these figures, there is not a linear relationship between whole-body arsenic concentrations and arsenic concentrations in the administered dose. For the less toxic organic arsenicals (cacodylic acid and Phytar-560), whole-body arsenic concentrations reached levels twice those of the inorganic arsenicals (As_2O_5 and As_2O_3) for similar arsenic levels in the administered dose. These results indicate that for the less toxic arsenic compounds, accumulation of elemental arsenic may proceed to higher levels in exposed organisms than for the more toxic inorganic arsenicals.

POWERLINE REVEGETATION

R. C. Dailman

R. Mowbray L. K. Mann

The prospect of nonchemical control of woody species on powerline rights-of-way requires new management techniques which will stabilize soil, eliminate hazardous trees, improve wildlife habitats, and minimize the need for herbicide applications. Grass-legume ground cover will partially satisfy these requirements by

Table 11.7. Vegetation composition and abundance in the first season after planting different species mixtures on powerline right-of-way

Species	Frequency ^a (%)	Number ^a	Dominance ^a	Importance ^a	Cover ^a (%)	Cover type
Bluegrass-legume treatment ^{b,c}						
Bluegrass ^d	56	450 ± 140 ^e	4.4	2.4	44 ± 16 ^e	Grass/legumes
Crabgrass	44	150 ± 56	4.9	2.2		
Kobe lespedeza ^{d,f}	88	540 ± 270	5.0	4.4		
Ladino clover ^{d,f}	34	36 ± 29	4.3	1.5		
Dogwood	6	14 ± 14	6.0	0.3	4 ± 4	Woody
Honeysuckle	17	14 ± 8	5.7	0.9	14 ± 8	Vine
Ragweed	11	11 ± 8	5.5	0.6	19 ± 5	Other
Fireweed	22	14 ± 7	5.8	1.3	82 ± 10	Total
Fescue-lespedeza treatment ^{b,c}						
Fescue	81	689 ± 93	5.7	4.7	34 ± 6	Grass/legumes
Broom sedge	15	17 ± 7	3.8	0.6		
Foxtail	13	23 ± 15	5.3	0.7		
Lespedeza ^d	57	89 ± 16	4.4	2.5	6 ± 4	Woody
Blackberry	2	1 ± 1	6.0	0.1	6 ± 3	Vine
Ragweed	4	2 ± 2	5.0	0.2	16 ± 3	Other
					61 ± 7	Total
Western grass treatment ^{b,c}						
Big bluestem ^d	4	68 ± 14	3.5	1.5	24 ± 5	Grass/legumes
Indian grass ^d	41	66 ± 15	3.3	1.4		
Switch grass ^{d,g}	59	120 ± 49	2.7	1.6		
Crabgrass	35	72 ± 24	5.7	2.0		
Panicum spp.	32	52 ± 12	3.6	1.2		
Lespedeza	21	67 ± 36	4.1	0.9	2 ± 1	Woody
Honeysuckle	3	3 ± 2	5.0	0.2	7 ± 3	Vine
Blackberry	8	5 ± 3	4.6	0.4		
Ragweed	29	32 ± 8	5.7	1.7	41 ± 6	Other
Fireweed	13	10 ± 4	4.5	0.6	74 ± 6	Total

^aDefinitions: *Frequency*, percentage of subplots on which species occurred; *Number*, mean individuals per subplot expressed per square meter; *Dominance*, mean relative value on a scale from 6 (highest) to 1 (lowest); *Importance*, represents dominance adjusted for total subplots per treatment; *Cover*, percentage of soil surface beneath cover-type canopy.

^bBluegrass (*Poa pratensis* L.), lespedeza [*Lespedeza striata* (Thumb) H. and A.] and ladino clover (*Trifolium repens* L.) were planted on three lower slopes. Data collected from 6-m² areas containing 18- to 154-cm² subplots. Fescue (*Festuca arundinacea* Shreb.) and lespedeza [*Lespedeza cuneata* (Dumont) G. Don.] were planted on four different slopes. Data collected from 18-m² areas containing 54 subplots. Western grasses included big bluestem (*Andropogon gerardi* Vitman), Indian grass [*Sorghastrum nutans* (L.) Nash.], and switch grass (*Panicum virgatum* L.), and were planted on four upper slopes. Data collected from 21-m² areas containing 63 subplots.

^cNot listed for bluegrass-legume, fescue-lespedeza, and western grass treatments were 12, 19, and 36 additional species, respectively.

^dPlanted species.

^ePlus or minus 1 standard error.

^fStatistics based on nine subplots.

^gStatistics based on 39 subplots.

restricting germination and seedling development of tree species. Herbaceous vegetation also will provide nutritious forage which will maximize wildlife and beef cattle utilization of rights-of-way. In cooperation with TVA Divisions of Power Construction and of Forestry, Fisheries, and Wildlife, three grass-legume mixtures (bluegrass-legume, fescue-lespedeza, and big bluestem-Indian grass-switch grass) were tested on six sites on the new powerline right-of-way crossing the AEC Reservation. Seed beds on diverse topographies (ridges, bottoms, slopes) were prepared and seeded in March and April 1971, and three months later percentage cover was estimated for different classes of vegetation (total, grass and legume, woody, vine, and other herbaceous cover). Relative dominance was estimated for the principal species.

Composition and species abundance for three different plantings are summarized in Table 11.7. Slope orientation was disregarded in this analysis. In terms of frequency, number, dominance, and other statistics, Kobe lespedeza accounted for a large fraction of the grass and legume cover on the bluegrass-legume treatment, and bluegrass, crabgrass, and ladino clover were other important species. Fireweed was the most important weed species on this treatment. Kentucky-31 fescue and *Sericea lespedeza*, the planted species, were responsible for most of the grass and legume cover on fescue-lespedeza treatment. Broom sedge and foxtail were of lesser importance, and fireweed was the most common weed. In the western grass treatment, crabgrass and ragweed were the most important species. The planted grasses were fairly abundant, but were dominated by weedy species in the first year.

Total cover varied from 61% in the fescue-lespedeza treatment to 82% for bluegrass-legume. Maximum grass and total cover were observed in the bluegrass treatment, and this response was attributed to higher site quality on lower slopes of highly dissected topography. In the first year, the grass-legume component accounted for half of total plant cover for plantings of cool-season species (fescue and bluegrass) while western grass seedlings comprised one-third of total cover. Weedy vegetation, particularly ragweed, ranked high in dominance and cover in all treatments. Invasion by weedy annuals, for example, ragweed, commonly occurs following disturbance on upland landscapes. It may be necessary to gage subsequent success of planted species (grass-legume treatments) in terms of second-order importance because grass tends to predominate later during intermediate stages of succession.

First-year results showed development of appreciable ground cover in all three treatments (60 to 80%) within

three months of planting, and from 30 to 50% of the cover vegetation contained the desired species. Planting to herbaceous vegetation readily achieved the management objective of stabilizing soil and reducing erosion. Greatest initial success for the bluegrass legume planting depended on the presence of Kobe lespedeza and appeared to be related to site quality. Success of western grass plantings will not be determined for several years because this length of time is required for completion of bluestem, Indian grass, and switch grass vegetative growth, after which time they will become more competitive with endemic species. Continued measurement of grass establishment on transmission line rights-of-way will determine if the introduced grasses can compete successfully with native shrubs. If successful, the nutritious western grasses will improve range quality and animal habitat, and these conservation efforts will lead to increased wildlife abundance through better management using native vegetation.

ECOLOGICAL ASSESSMENT RELATED TO THE FEDERAL REPOSITORY

R. C. Dahlman Y. A. Tanaka

The proposed federal repository at Lyons, Kansas, represents a new approach for isolating large quantities of radioactive waste from the biotic environment. As a radioactive waste management procedure, the practice is new and untested; therefore, the Kansas facility has been designated by the AEC as a "demonstration repository." Ecological investigations during early phases of the project are designed to establish baselines and methodologies which can be applied in later assessment of possible impact on the environment. Results from ecological studies will provide a framework for assessing alleged or real impacts such as (1) long-term biological effects from either chronic or accidental releases of radioactivity, particularly ^{90}Sr , ^{137}Cs , and Pu. Environmental pathways of these radionuclides in affected ecosystems will be examined for possible concentration in food chains, a process which could cause hazardous levels of radioactivity in biota and man. Another potential impact concerns (2) possible thermal effects on surface biota manifested by heat dissipation from high-level waste deposits.

Preliminary information on ecological, agricultural, and environmental factors has been assembled for the Environmental Quality Statement and the Safety and Hazards Analysis Report on the proposed repository. Initial efforts have focused on: (1) a visit to the site in 1970, (2) ecological surveys which were carried out by consultants from Kansas State University, (3) identifi-

cation of possible environmental pathways of radionuclide movement, (4) formulation of predictive models for estimating radioactivity concentrations in ecosystem components, and (5) summarization of meteorological conditions for the Central Kansas region. Background information collected during this phase of assessment has been used to characterize agricultural and ecological conditions, to establish conceptual designs for evaluating impact from long-term operations, and to define additional research tasks for collecting missing ecological information.

One phase of preliminary assessment has focused on the expected behavior of ^{90}Sr in a generalized grassland ecosystem. Bluestem grassland has been recommended for the 1000-acre site because its establishment would enhance stability and control management influences over long-term periods of postoperation surveillance. A predictive model of ^{90}Sr dynamics in plant-soil-litter of grassland was formulated from best available literature data. Based on estimated low-level continuous release of ^{90}Sr from the facility, change in concentration in the plant-soil-litter segment was calculated for various time intervals after initiation of repository operations.¹⁷ Radiostrontium may increase by a factor of 3 in the litter component and by 50% in living vegetation according to this simulation (Fig. 11.8). New equilibria will become established in these components within three years, after which time concentrations would diminish as physical decay rates exceed rate of new input to the system.

Predictive modeling procedures will apply to both chronic and acute inputs providing transfer parameters are based on "pulse" experimental data. Such efforts can estimate various secondary radioactivity source terms (foliage, root, litter) which, in turn, serve as potential inputs to ecological and agricultural food chains. While this simulation describes radiostrontium dynamics in the grass-litter-soil component, similar modeling techniques will be used to illustrate radionuclide movement or concentration for other organisms and pathways of the ecosystem. Specific activity models will be applied to aquatic and terrestrial situations when sufficient information exists on the stable chemistry of the environments and organisms. Other phases of radioactivity assessment will involve radionuclide movement through environmental pathways of aquatic and agroecosystems.

Dissipation of waste heat from high-level wastes may cause a small increase in temperature at the soil surface.

However, heat flux from deposited wastes of ten times the geothermal rate is not expected to change the surface temperature more than a fraction of a degree Fahrenheit, a negligible amount when compared with observed daily and seasonal variations. Daily bi-directional radiation flux in the soil surface ranges from 0 to 0.1 cal/cm², and this is at least 1000 times greater than the predicted heat flux from waste deposits. Compared with calculations in radiant energy balance and resultant soil heat flux, the increases in the surface temperature from waste heating are expected to be small or negligible. Specific low-intensity effects on energy balance components include: (1) Net radiation (R_n) would decrease slightly, possibly 0.01 langley/min, because outgoing long-wave radiation is proportional to the fourth power of the surface temperature. (2) Evapotranspiration could be affected by a 10% increase in the vapor pressure gradient, one factor of the

Fig. 11.8. Change in ^{90}Sr concentration for plant-soil segment of a grassland ecosystem following chronic deposition of $0.86 \text{ pCi m}^{-2} \text{ day}^{-1}$. Values corrected for decay. Note different scale for soil compartment and for 10^3 to 10^4 time interval. Decrease was nearly linear from 10^3 to 10^4 days.

17. R. C. Dahlman et al., ORNL-TM-3619.

evaporation equation. Other complex processes affect evaporation, but only some of them are directly influenced by temperature. (3) Sensible heat fluxes of air and soil which are also dependent on several factors (e.g., water, eddy diffusivity, conductance, soil texture, and organic content). Thus, specific effects of additional heat are not easily identified. That physical and biotic effects could occur from an increased geothermal flux does not necessarily mean that devastating consequences will result. Identification of potential impacts will be followed by more detailed research on those manifestations which substantively could be detrimental over centuries of biotic exposure to such a heat source.

An ecology research program is being designed to provide technical information for assessing conceivable chronic or accidental impacts on biotic populations, ecosystems, and man during repository operations and periods of postoperation surveillance. Onsite ecological investigations will determine the structure and function of affected ecosystems and will examine those ecological processes which may influence radionuclide fluxes in the vicinity of the waste repository. Baseline references will be compiled and used to evaluate thermal or radioecological effects (either real or alleged) related to routine operations or emergency situations. Many tasks, by necessity, will be carried out at the repository site or in adjacent agroecosystems, and the work probably will be performed by ecologists from the state of Kansas. Field data on aquatic and terrestrial ecosystem processes will be combined with general concepts of radionuclide metabolism in organisms and with existing information on the behavior of radioactivity in the environment. Ecological research data will be coupled with ecosystem models to predict the fate of chronically or accidentally released radioactivity in the environment.

CADMIUM STUDIES WITH BLUEGILL (*LEPOMIS MACROCHIRUS*)

M. S. Hibbs G. U. Urickson

Cadmium is one of the most toxic metals to living systems, particularly to aquatic organisms. Because of the potential pollutional significance of this element, a series of studies were initiated to determine an approximate LD_{50} , uptake, elimination, and distribution of cadmium in bluegills. Cadmium-109 was used as a tracer in the latter two studies.

PROCEDURES

Modified LD_{50} Studies

Five fingerling bluegills 2 to 4 in. long were placed in each aquarium containing 18 liters of stream water and given a single dose of 1, 5, or 10 ppm of Cd in the chloride form. The temperature was maintained at $20 \pm 1.0^\circ\text{C}$.

The fish were acclimated for two weeks before use and were held in a 45-gal aquarium, temperature $20 \pm 0.5^\circ\text{C}$.

Elimination studies. Bluegills (3 to 5 in.) were given oral injections of $0.25 \mu\text{Ci}$ of $^{109}\text{Cd}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ using 3 cm of polyvinyl tubing attached to a 2-cm³ tubulin syringe inserted through the esophagus into the gullet.

The initial quantity of ^{109}Cd retained was based on an initial determination of ^{109}Cd present 1 hr after injection. Cadmium-109 retention was determined at 1, 2, 4, 7, 9, and 11 days after injection. All radiation measurements were made using a multichannel analyzer with an NaI(Tl) detector.

Uptake experiments. Five fingerling bluegills were placed in each aquarium containing 5 liters of stream water tagged with $9.9 \mu\text{Ci}$ of ^{109}Cd . Uptake was determined at intervals of $\frac{1}{4}$, 1, 2, 4, 7, 10, and 14 days. The temperature was $21.0 \pm 0.5^\circ\text{C}$.

Internal distribution of ^{109}Cd . Bluegills were administered ^{109}Cd in an analogous manner as in the elimination studies. Fish were whole-body counted, then sacrificed at intervals of 2 hr, 1, 2, 4, 7, 9, 14, and 21 days. The fish were dissected, and the ^{109}Cd concentration was determined for each organ.

DISCUSSION

The modified LD_{50} studies established a definite toxicity of Cd to bluegills (*Lepomis macrochirus*). LD_{50} 's of 19 days for 5 ppm and 2.0 days for 10 ppm of Cd in the chloride form were obtained, indicating a logarithmic increase in mortality as the concentration is doubled (Table 11.8). These data represent toxic effects when a fish is exposed to a single dose of Cd, a condition unusual in the natural environment where a continual exposure rate is more probable. A more practical LD_{50} of 24 hr for 4.56 ppm Cd is obtained when fish were given a continual dose using a constant diffusion device.¹⁸

18. Q. H. Pickering and C. Henderson, pp. 578-81 in *Proceedings of the 19th Industrial Waste Conference*, Purdue University, 1964.

The toxic form of Cd in aquatic systems is not known. Its chemical properties would indicate that Cd enters aquatic systems in the form of a divalent water-soluble salt, such as CdCl_2 or $\text{Cd}(\text{NO}_3)_2$. If this is true, it would be possible for the dissociated Cd^{2+} ion to form coordination compounds with organic and inorganic material present in the water supply. The determination of an exact exposure concentration is difficult due to immobilization; thus the toxic threshold of fish to Cd may be lower than present data indicate.

Uptake of Cd by bluegills occurs rapidly as indicated by Fig. 11.9. Maximum uptake was obtained by the fourth day, after which an equilibrium between the Cd levels in the water and in the fish was attained. The

Table 11.8. Results of modified LD_{50} studies
As the concentration is doubled, the toxicity increases by a factor of 10.

	Concentration	
	5 ppm Cd	10 ppm Cd
Number of fish	11	10
Mean death time (days)	17.091	8.16
Standard deviation	8.8	9.9
LD_{50} (days)	19.0	2.0

Fig. 11.9. The uptake of ^{109}Cd by fingerling bluegills (2 to 4 g) from water.

Fig. 11.10. Retention of ^{109}Cd by bluegills.

problem of a single dose may make the data somewhat misleading, since uptake, under conditions where a continual rate of exposure is available, may continue beyond the first days of exposure.

In experiments where Cd was not present in the environment, a rapid elimination was found to occur (Fig. 11.10). A biological half-life of 3.68 days was obtained after a single dose. While these results agree with those for *Gambusia*,¹⁹ they are inconsistent with the half-life of 25 to 400 days obtained for mammals,²⁰ and that of three to four weeks²¹ for the guppy (*Lebistes reticulatus*). The short biological half-life obtained is analogous to the rapid elimination phase observed in the bioelimination of radionuclides from the sunfish, *Lepomis gibbosus*.²²

Examination of the internal distribution of Cd indicates that it is incorporated in all the body tissues, but not in equal concentrations (Table 11.9). The appreciable lack of concentration in the brain indicates that the nervous system is an improbable site of Cd

19. R. Gaskins, G. Stein, and R. Roberts, Oak Ridge National Laboratory, personal communication.

20. L. Friberg, M. Floman, and G. Norberg, *Cd in the Environment: A Toxicological and Epidemiological Appraisal* (to be published).

21. L. Larsson and A. Jernstam, *Ecological Research Committee Bulletin No. 5*, Swedish Natural Science Research Council, Stockholm, Sweden, 1969.

22. M. Marini, F. Argentei, A. Borg, A. Brunetti, R. Orlandi, and G. Pozzi, *Radionuclides in Ecosystems*, UNBEC CONF-710501 (in press).

action. Significant concentration of Cd was noted in the gills, which may indicate that Cd interferes with the permeability of the gills.

High concentrations of Cd were found in the gastrointestinal tract. The concentration in the stomach remains essentially constant. Cadmium is concentrated in the pyloric caeca, then released slowly. The concentration of Cd in the pyloric caeca is four times greater than its concentration in the stomach. No significant

pattern of concentration or elimination was noted for the intestines. The major concentration of Cd, outside the gastrointestinal tract, is found in the liver and kidney, which is consistent with studies of Cd distribution in mice.²³

23. M. Merlini and S. Ulberg, *Arch. Environ. Health* 7, 686-94 (1963).

Table 11.9. Internal distribution of ¹⁰⁹Cd in bluegills
The concentration index is expressed as percent total picograms/percent total body weight.

Organ	hr		days					
	2	24	2	4	7	9	14	21
Gonads								
Male		1.19						0.32
Female	0.48			0.22	0.21	6.01	27.85	
Heart	1.39	0.60	0.16	3.40	1.15	2.07	17.73	6.73
Liver	1.80	0.53	2.97	7.85	11.05	2.90	5.86	10.37
Kidney	3.07	1.62	4.11	12.60	11.30	4.30	12.78	19.13
GI tract	13.05	33.85				27.00		
Gall bladder			1.13	1.16	4.87	0.48	33.00	9.25
Pyloric caeca			45.39	91.46	94.31		44.68	52.27
Stomach				28.03	17.72		21.35	16.18
Intestines			18.79	41.10	14.10		9.42	33.65
Pancreas				3.60	6.40		2.73	6.60
Gill	5.47	18.31	0.68	1.32	1.57	0.90	2.67	1.17
Eyes	0.14	0.02	0.01	0.10	0.22	0.07	0.20	1.18
Brain	0.01		0.05	0.26	0.57	0.04		15.46
Residue	0.39	0.03	0.04	0.15	0.09	0.11		0.19

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Radionuclide Dynamics in Insect Food Chains, Annual Meeting, Canadian Entomological Society, August 23-24, 1970, Winnipeg, Canada.

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Effects of Beta-Gamma Radiation on Earthworms Under Simulated Fallout Conditions, U.S. Atomic Energy Commission-Office of Civil Defense Symposium "Survival of Food Crops and Livestock in the Event of Nuclear War," September 15-19, 1970, Brookhaven National Laboratory, Upton, Long Island.

Interpretation of Data in Ecosystem Synthesis: Energy and Nutrient Flux in Terrestrial Invertebrates, International Biological Program Symposium, Annual Meetings, American Association for the Advancement of Science, December 27-31, 1970, Chicago, Illinois.

Systems Analyses as Applied to Ecological Processes, International Biological Program, Taiga Workshop, June 12-20, 1971, Stockholm, Sweden.

Foliage Production and Consumption in the Forest Canopy, Annual Meeting, American Institute of Biological Sciences, August 20-September 3, 1971, Fort Collins, Colorado.

D. E. Reichle, R. I. Van Hook, Jr., and R. A. Goldstein

Foliage Production and Consumption in a Forest Canopy, Annual AIBS Meeting, August 28-September 3, 1971, Fort Collins, Colorado.

F. G. Taylor and J. P. Witherspoon

Retention of 1-44 μ Fallout Particles by Soybean and Sorghum Plants, Association of Southeastern Biologists Annual Meeting, April 15, 1971, Richmond, Virginia.

G. U. Ulrikson

Environmental Information System, Ecological Sciences Division Annual Information Meeting, Oak Ridge National Laboratory, March 3-5, 1971.

Radiation Effects on Serum Proteins, Hematocrits, Electrophoretic Patterns, and Protein Components, Third National Symposium on Radioecology, May 10-12, 1971, Oak Ridge, Tennessee.

Environmental Information System, ORNL-NSF Environmental Program: Annual Information Meeting, Oak Ridge National Laboratory, September 27, 1971.

G. U. Ulrikson and C. C. Coutz:

Thermal Effects Studies, Ecological Sciences Division Annual Information Meeting, Oak Ridge National Laboratory, March 3-5, 1971.

G. U. Ulrikson and H. Guderly

The Effects of Sublethal Thermal Shock on the Blood Serum Proteins of the Rainbow Trout (Salmo gairdneri), Third National Symposium on Radioecology, May 10-12, 1971, Oak Ridge, Tennessee.

R. I. Van Hook

Nutrient Dynamics in Arthropod Components of a Grassland Ecosystem, AIBS Meeting, August 1970, Bloomington, Indiana.

Survivorship of Crickets: Acheta domesticus (L.), as Affected by Variations in Gamma Dose Rate, Symposium on the Survival of Food Crops and Livestock in the Event of Nuclear War, September 15-18, 1970, Brookhaven National Laboratory.

Energy and Nutrient Turnover in a Grassland Ecosystem, Entomological Society of America Annual Meeting, November 1970, Miami Beach, Florida.

The Role of Arthropods in Mineralization of Detritus, Conference on the Role of Detritus in Ecosystems, April 1971, University of Georgia, Athens, Georgia.

Effects of Gamma Radiation and Temperature on the Biological Assimilation and Retention of Cesium-137 by Acheta domesticus (L.), Annual Meeting of the Association of Southeastern Biologists, April 1971, Richmond, Virginia.

Effect of Gamma Radiation on the Life Stages of the Migratory Grasshopper, Melanoplus sanguinipes (F.), Third National Symposium on Radioecology, May 10-12, 1971, Oak Ridge, Tennessee.

Investigations of Arthropods Food Chain Dynamics: Radioisotope Techniques, AIBS Meeting, August 1971, Fort Collins, Colorado.

J. P. Witherspoon

Field Studies of Fallout Retention by Plants, Symposium on Survival of Food Crops and Livestock in the Event of Nuclear War, September 16, 1970, Brookhaven National Laboratory, Upton, New York.

Transfers of Cesium-134 from a Tree Canopy to Understory Vegetation, Association of Southeastern Biologists Annual Meeting, April 15, 1971, Richmond, Virginia.

LECTURES

S. I. Auerbach

What Is This Thing Called Ecology and Why Is It So Important in the Seventies, East Tennessee Chapter-Health Physics Society Meeting, Oak Ridge Country Club, November 19, 1970, Oak Ridge, Tennessee.

Ecological Considerations Concerning Nuclear Power Plant Siting, Physics Division Seminar, Oak Ridge National Laboratory, November 20, 1970, Oak Ridge, Tennessee.

Pollution, Republican Women's Club, January 14, 1971, Knoxville, Tennessee.

Pollution, Central Methodist Church, February 14, 1971, Knoxville, Tennessee.

Nuclear Energy and Man, League of Women Voters, April 20, 1971, Oak Ridge, Tennessee.

Effects of Technological Development, U.S. Civil Service Commission, Executive Seminar Center, August 26, 1971, Oak Ridge, Tennessee.

The Case for Survival, Alabama Tuberculosis Association, October 12-13, 1971, Birmingham, Alabama.

B. G. Blaylock

Radiation Effects on Aquatic Systems, Radiation Ecology Class, University of Tennessee, February 24, 1971, Knoxville, Tennessee.

Radiation Effects on Aquatic Systems, Tennessee Technological University, Tech Aqua Project, July 3, 1971, Center Hill.

Cytogenetic Effects of Tritiated Water in Chironomus, University of Tennessee, Institute of Radiation Biology, April 27, 1971, Knoxville, Tennessee.

Robert L. Burgess

The Need for Natural Areas, University of Montana, April 1, 1971, Missoula, Montana.

Citizen's Groups and Environmental Quality, University of Montana, April 1, 1971, Missoula, Montana.

The International Biological Program, University of Montana, April 2, 1971, Missoula, Montana.

The Environment - Government, Scientists, and Citizens, Bismarck Junior College, May 3, 1971, Bismarck, North Dakota.

A Quality Human Environment, Academic Year Institute, University of South Dakota, May 6, 1971, Vermillion, South Dakota.

The International Biological Program, University of South Dakota, May 6, 1971, Vermillion, South Dakota.

Careers in Environmental Science, Academic Year Institute, University of South Dakota, May 7, 1971, Vermillion, South Dakota.

Environment and Life in the Northern Great Plains, Summer Institute for College Teachers, Minot State College, August 19, 1971, Minot, North Dakota.

The International Biological Program, Minot State College, August 19, 1971, Minot, North Dakota.

The Destruction of North Dakota, Summer Institute for College Teachers, Minot State College, August 20, 1971, Minot, North Dakota.

Ecology and New Product Potential, Third Annual Agri-Business Convention, American Marketing Association, November 11, 1971, Omaha, Nebraska.

C. C. Coutant

Thermal Effects, ORAU Panel Discussion on Environmental Effects of Nuclear Power Plants, August 4, 1970, Oak Ridge, Tennessee.

Water Pollution, ORAU Environmental Assessment Course, August 20, 1970, Oak Ridge, Tennessee.

Columbia River Thermal Effects Studies, Second Thermal Pollution Seminar, sponsored by the Institute for Environmental Sciences, September 23, 1970, Oak Ridge, Tennessee.

Ecological Effects of Power Plant Cooling, Symposium on Ecological Problems in the Marine Environment, First National Biological Congress, November 10, 1970, Oak Ridge, Tennessee.

Thermal Effects of Nuclear Power Plants, Seminar to ORNL Participants from the Great Lakes Colleges Association, October 12, 1970, Oak Ridge, Tennessee.

Quantitative Analysis of Effects of Thermal Shock on Young Salmonids, Seminar to Graduate Program in Ecology, University of Tennessee, October 15, 1970, Knoxville, Tennessee.

Panel Discussion on Environmental Effects of Nuclear Power Plants, Citizens Group from Midland, Michigan, November 9, 1970, Oak Ridge, Tennessee.

Effects of Pollution on Ecology of Streams, ORAU Environmental Assessment Course, November 20, 1970, Oak Ridge, Tennessee.

The of Thermal Discharges for Enhancing Aquaculture, European Inland Fisheries Advisory Committee Workshop, sponsored by FAO, Stuttgart, Arkansas, September 10, 1970.

Thermal Effects Studies, Two seminars presented to faculty and staff, Laboratory of Limnology, University of Wisconsin, January 20 and 21, 1971, Madison, Wisconsin.

Review of Entrainment Research, Biological Entrainment Workshop, sponsored by the Chesapeake Bay Cooling Waters Study group, Johns Hopkins University, January 24–26, 1971, Baltimore, Maryland.

Coexisting with Nuclear Energy – Thermal Effects, ORNL Physics Division Seminar, January 8, 1971, Oak Ridge, Tennessee.

Thermal Pollution, ORAU Special Training Course in Environmental Aspects of Radiation Sciences, January 13, 1971, Oak Ridge, Tennessee.

Thermal Effects Research by AEC, National Academy of Engineering, Committee on Power Plant Siting, Water Working Group, February 22, 1971, Washington, D.C.

Thermal Pollution, Earth Day talk, University of Tennessee, April 21, 1971, Knoxville, Tennessee.

Thermal Effects Research by AEC, Class lecture, University of Tennessee, April 23, 1971, Knoxville, Tennessee.

The Environment and Nuclear Power: Thermal Effects, ORAU Seminar for Representatives of Utilities, May 25, 1971, Oak Ridge, Tennessee.

Thermal Effects, ORAU Seminar for AEC Demonstrators on Public Tour, August 18, 1970, Oak Ridge, Tennessee.

Thermal Effects, Ecological Enrichment Program for Chemists, ORAU, August 24, 1970, Oak Ridge, Tennessee.

R. C. Dahlman

Nitrogen Dynamics in the Grassland Ecosystem, Division of Biology, Kansas State University, March 22, 1971, Manhattan, Kansas.

P. B. Dunaway

Radionuclides as Tools for Ecological Research, Pymatuning Laboratory of Ecology, University of Pittsburgh, July 21, 1970, Linesville, Pennsylvania.

Radioisotope Techniques in Vertebrate Ecology, University of Tennessee Radioecology Course, February 3, 1971, Oak Ridge, Tennessee.

Radioisotope and Irradiation Studies with Mammals, Department of Zoology, Michigan State University, May 26, 1971, East Lansing, Michigan.

J. W. Elwood

Aquatic Ecology at the Oak Ridge National Laboratory, Institute of Biological Research, September 3, 1971, Belgrade, Yugoslavia.

R. A. Goldstein

Ordination and Classification of Ecosystems, Systems Ecology Program, San Diego State College, April 1971, San Diego, California.

J. M. Hett

Age Structural Dynamics of Balsam Fir and Eastern Hemlock, Department of Botany Seminar, University of Georgia, November 16, 1970, Athens, Georgia.

Reproductive Dynamics, Systems Modeling Section of the Forest Service Leadership School, June 23, 1971, Madison, Wisconsin.

Use of Time-Sharing Computer for Land-Use Simulation, Systems Modeling Section of the Forest Service Leadership School, June 24, 1971, Madison, Wisconsin.

S. V. Kaye

Radioecology and Peaceful Uses of Atomic Energy, University of Tennessee Radioecology Course, February 17, 1970, Oak Ridge, Tennessee.

Modeling Dose Commitments Based on Mineral Flows in a Tropical Ecosystem, Argonne Symposium on the Analysis and Synthesis of Ecological Systems, Argonne National Laboratory, October 26-28, 1970, Argonne, Illinois.

Systems Analysis Techniques for Predicting Dose to Man from Radioactivity Released to the Environment, IAEA Headquarters, August 30, 1971, Vienna, Austria.

Environmental Systems Analysis, Biology Division, Euratom Laboratory, September 2, 1971, Ispra, Italy.

Evaluating Environmental Releases of Radioactivity, Headquarters of Italian National Committee on Nuclear Energy, September 6, 1971, Rome, Italy.

Ecology and Wise Use of Natural Resources, Camp Tremont, September 17, 1970, Great Smoky Mountains National Park.

D. J. Nelson

Technology Assessment and Watershed Research, Oak Ridge Associated Universities, September 30, 1970, Oak Ridge, Tennessee.

Predicting Radionuclide Uptake Aquatic Ecosystems, Citizens Panel from Midland, Michigan, November 9, 1970, Oak Ridge, Tennessee.

Ecological Research, Oak Ridge High School, November 16, 1970, Oak Ridge, Tennessee.

Ecological Effects of Nuclear Power Reactors, DeFauw University, January 15, 1971, Greencastle, Indiana.

Biogeochemistry of Clams, Department of Geology and Geography, University of Tennessee, February 1, 1971, Knoxville, Tennessee.

Cycling and Effects of Radionuclides in Aquatic Ecosystems, Ecology Program, University of Tennessee, February 3, 1971, Oak Ridge, Tennessee.

Aquatic Ecology Studies at ORNL, General Engineering and Construction Division Seminar, March 10, 1971, Oak Ridge, Tennessee.

Radioactive Materials and the Environment, Special Training Division, Oak Ridge Associated Universities, March 31, 1971, Oak Ridge, Tennessee.

Aquatic Ecology, Special Training Division, Oak Ridge Associated Universities, April 8, 1971, Oak Ridge, Tennessee.

Analytical Needs for Ecological Sciences, Analytical Chemistry Division Seminar, May 20, 1971, Oak Ridge, Tennessee.

Radionuclide Cycling, Special Training Division, Oak Ridge Associated Universities, September 2, 1971, Oak Ridge, Tennessee.

Aquatic Ecology, Special Training Division, Oak Ridge Associated Universities, September 2, 1971, Oak Ridge, Tennessee.

Radionuclides in Aquatic Systems, University of Pittsburgh, September 30, 1971, Pittsburgh, Pennsylvania.

J. S. Olson

Systems Ecology, Lund University, September 2, 1970, Lund, Sweden.

Ecological Modeling, Uppsala University, September 9, 1970, Uppsala, Sweden.

Integrated Research on Terrestrial Productivity - Systems and Subsystem Studies, Biological Institute, September 21, 1970, Belgrade, Yugoslavia.

Data and Models of Biospheric Change, Panel on Computation, Decision Making, and the Environment, Spring Joint Computer Conference, May 19, 1971, Atlantic City, New Jersey.

R. V. O'Neill

A Typology of Ecological Models, Resources for the Future, November 1970, Washington, D.C.

Error Analysis Methods, Mathematics Division, Oak Ridge National Laboratory, March 1971, Oak Ridge, Tennessee.

Modeling and Systems Analysis in Ecology, University of Tennessee Research Station, March 1971, Oak Ridge, Tennessee.

D. E. Reichle

Ecological Research Programs at Oak Ridge National Laboratory, Joint Conference with State Environmental Agencies, October 28, 1970, Nashville, Tennessee.

Oak Ridge National Laboratory Ph.D. Recruitment Program, University of California, Berkeley, January 1, 1971, Berkeley, California; Stanford University, January 22, 1971, Stanford, California; University of Wisconsin, November 15, 1971, Madison, Wisconsin.

U.S. IBP Deciduous Forest Biome, Tokyo Metropolitan University, January 10, 1971, Tokyo, Japan; Osaka University, January 11, 1971, Osaka, Japan; University of Malaysia, January 13, Kuala Lumpur, Malaysia; Symposium on Tropical Ecology, January 14–20, New Dehli, India.

Spring Mating Calls of the Amphibia, Ecology Explorer Post, March 9, 1971, Oak Ridge, Tennessee.

Primary Production in Gaseous Exchange IBP Research at Oak Ridge, Duke University, May 25, 1971, Durham, North Carolina.

Transport and Fate of Radionuclides in the Environment, Cooperative Science Education Center, NSF-SSTP Summer Institute in Radiation and Its Biological Consequences, July 3, 1971, Oak Ridge, Tennessee.

Program and Objectives of the Oak Ridge IBP Site, Cowetta Hydrologic Laboratory, July 15, 1971, Franklin, North Carolina.

Environmental Ethics, Oak Ridge Unitarian Church, September 12–November 28, 1971, Oak Ridge, Tennessee.

Integrated Environmental Research, UT Graduate Program in Ecology, Plant Ecology Class, November 7, 1971, Oak Ridge, Tennessee.

J. P. Witherspoon

Ecology and the Environmental Crisis, Science Day, Carson Newman College, November 2, 1970, Jefferson City, Tennessee.

Radiation Ecology, Oak Ridge High School Biology Classes, November 4, 1970, Oak Ridge, Tennessee.

Education in Ecology, Environment 2000 Program, University of Tennessee, February 6, 1971, Knoxville, Tennessee.

Ecological Sciences at ORNL, Tennessee Junior Science and Humanities Symposium, ORNL, March 5, 1971, Oak Ridge, Tennessee.

What is Ecology?, East Tennessee Section of the Society of Manufacturing Engineers, February 4, 1971, Oak Ridge, Tennessee.

Ecology and the Environment, East Tennessee Section of IEEE, March 9, 1971, Knoxville, Tennessee.

Radiation Ecology, Convo-71 of the United Methodist Church, March 25, 1971, Knoxville and Oak Ridge, Tennessee.

Radiation Ecology, Institute of Radiation Biology Seminar, University of Tennessee, April 12, 1971, Knoxville, Tennessee.

Radiation Botany, Biology Division Seminar, ORNL, May 7, 1971, Oak Ridge, Tennessee.

Ecology at ORNL, Tennessee Technological University, July 22, 1971, Cookeville, Tennessee.

Radioactivity in Ecosystems, Applied Ecology Institute for Teachers, ORAU, September 1, 1971, Oak Ridge, Tennessee.

Ecology at ORNL:

Biology Class, December 3, 1970, Mars Hill College.

Biology Class, May 1, 1971, Eastern Kentucky University.

Physics Class, May 7, 1971, North Georgia College.

M. Witkamp

Microbial Ecology, January 18–February 5, 1971, Department of Biology, University of Puerto Rico, Rio Piedras, Puerto Rico, in the series "Modern Topics in Biology."

Microbiology in the IBP, School of Medicine, Puerto Rico Nuclear Center, and Department of Biology, University of Puerto Rico, February 3, 1971, Rio Piedras, Puerto Rico.

Mineral Release from Decomposing Forest Litter, Decomposer Conference, April 1–2, 1971, Athens, Georgia.

Mineral Flux in Model Systems and in the Field, Seminar on Microbial Contribution to Terrestrial Ecosystem Energy Flow and Nutrient Cycling, 71st Annual Meeting of the American Society of Microbiology, May 6, 1971, Minneapolis, Minnesota.

Microbial Transfer of Minerals in Forest Ecosystems, Forest Service Leadership School Symposium on Systems Ecology, June 21–22, 1971, Madison, Wisconsin.

THESES**Carol Macklin**

Decomposition of Leaf Litter from Tulip Poplar (Liriodendron tulipifera L.) Trees Defoliated with Cacodylic Acid, M.S. thesis, Department of Biology, Emory University, Atlanta, Georgia, May 27, 1971.

J. B. Mathies

Annual Consumption of Cesium-137 and Cobalt-60 Labeled Pine Seeds by Small Mammals in an Oak–Hickory Forest, Ph.D. thesis, Michigan State University, East Lansing, Michigan (1971).

H. H. Shugart

The Niche Hyperspace Concept and Habitat Selection of Winter Fringilids in Northern Georgia, Ph.D. thesis, University of Georgia Zoology Department, Athens, Georgia, 68 pp. (1971).

PROFESSIONAL ACTIVITIES**S. I. Auerbach**

Director, Eastern Deciduous Forest Biome, Analysis of Ecosystems, International Biological Program.

Vice Chairman, Executive Committee, U.S. National Committee for the IBP.

President, Ecological Society of America.

Member, U.S. National Committee of the International Union of Biological Sciences.

Member, Special Committee on Biological Water Quality of the Ohio River Valley Water Sanitation Commission.

Member, National Academy of Engineering Committee on Power Plant Siting.

Member, Editorial Board of *International Journal of Environmental Sciences*.

Member, Editorial Board of *Radiation Botany*.

Member, Advisory Board, *Advances in Radiation Biology*.

Member, Board of Trustees, The Institute of Ecology.

Member, Board of Ecological Advisors of the Bureau of Reclamation.

Participant in AEC educational film entitled "No Turning Back."

Robert L. Burgess

President, North Dakota Academy of Science, 1970-71.

Chairman of Session: Early Results in the Eastern Deciduous Forest Biome, US-IBP, 24th Annual AIBS Meeting, September 2, 1971, Colorado State University, Fort Collins, Colorado.

Member, Program Review Committee, Grasslands Biome, US-IBP, June 6, 1971, Colorado State University, Fort Collins, Colorado.

Member, Program Review Committee, Desert Biome, US-IBP, June 9, 1971, Utah State University, Logan, Utah.

Member, Membership Committee, Ecological Society of America, 1965-present

Member, North Dakota Wildlife Advisory Committee, 1967-present.

Review Editor, *Ecology*, 1970-present.

C. C. Coutant

National Academy of Sciences, Water Quality Criteria Revision Project, Member of Panel on Freshwater Aquatic Life and Wildlife (1971). Author of section on "Temperature."

National Academy of Engineering, Committee on Power Plant Siting, Member of Water Working Group (1971).

Electric Power Council on Environment, Water Research Coordinating Committee.

Member of Research Committee, Water Pollution Control Federation.

Co-Chairman, Environmental Action Council of Oak Ridge (1971).

R. C. Dehman

Discussion leader on Nitrogen Cycling and Modeling at Workshop on Nitrogen Dynamics in Ecosystems, October 13-16, 1971, University of Georgia, Athens, Georgia.

P. B. Dunaway

Member of Site Review Team at Savannah River Plant for AEC.

Member of Committee on Anatomy and Physiology, American Society of Mammalogists.

N. T. Edwards

Participant in IBP Decomposition Workshop, North Carolina State University, Raleigh, North Carolina, February 1971.

J. W. Elwood

Visited the Institute of Biological Research in Belgrade and Titograd, Yugoslavia, and proposed IBP study sites at Lake Skadar and the Lower Danube River in Yugoslavia, August 30-September 3, 1971.

R. A. Goldstein

Participant, Biological Systems Simulation Group Work Conference, January 17-21, 1971, Gainesville, Florida.

Participant at Eastern Deciduous Forest Biome, IBP Workshops on Primary Productivity, Duke University, 1970; Meteorology and Hydrology, University of Wisconsin, September 1970; and Modeling, University of Wisconsin, October 1970.

W. F. Harris

Member, AIRS Visiting Radiation Biologists Program.

Process Coordinator, Terrestrial Primary Production, Eastern Deciduous Forest Biome, US-IBP.

Member, Interbiome Primary Productivity Committee, US-IBP.

Participated in Boy Scouts' Nature Study Camporee, May 1, 1970, Norris, Tennessee.

"Ecological Research at ORNL" field tour and discussion to:

1. Personnel, Forestry and Wildlife Division, TVA, ORNL, March 25, 1971 (with G. S. Henderson),
2. Ecology class, Brigham Young University, ORNL, April 6, 1971 (with D. E. Reichle),
3. Hydrology class, University of Georgia, ORNL, May 19, 1971 (with G. S. Henderson),
4. Forest management class, University of Tennessee, June 14, 1971 (with G. S. Henderson),
5. Recreation and wildlife class, University of Tennessee, ORNL, July 12, 1971 (with G. S. Henderson).

G. S. Henderson

Participant, Decomposition Workshop, North Carolina State University, Raleigh, North Carolina, February 19-20, 1971.

Participant, Detritus Conference, University of Georgia, Athens, Georgia, April 1-2, 1971.

Participant, IBP Eastern Deciduous Forest Process Coordinators Meeting, August 5, 1970.

Advisor to Pre-coop students, Summer.

Conducted tour of Walker Branch Watershed for University of Tennessee Forestry classes (with W. F. Harris), May 19 and June 14, 1971.

J. M. Hett

Participant, IBP Workshop on Primary Productivity, Duke University, July 23-25, 1970, Durham, North Carolina.

Participant (Full time), Interdisciplinary Study on the Aleut Adaptation to the Bering Land Bridge Coastal Configuration, directed by W. S. Laughlin, J. S. Aigner, and R. F. Black, University of Connecticut, Storrs, Connecticut, sponsored by NSF, July 1-August 31, 1971.

S. V. Kaye

Organized Ecology Program for Fall Conservation Camporee, Boy Scouts of America, Camp Chota, Norris, Tennessee. Staff members presenting lectures included: J. P. Witherspoon, P. B. Dunaway, S. V. Kaye, F. G. Taylor, D. E. Reichle, and W. F. Harris.

Served as Chairman of Project SGAR (Save Our American Resources), Pellissippi District, Great Smoky Mountain Council, Boy Scouts of America. Numerous conservation and pollution abatement projects were undertaken, including tree plantings (approximately 7,000 seedlings), an antilitter day (18 truck loads of litter collected), and trail clearing.

Task group member of Committee 4 on Application of Recommendations, International Commission on Radiological Protection.

Official Observer, United States Delegation to Fourth International Conference on the Peaceful Uses of Atomic Energy, Geneva, Switzerland, September 6-16, 1971.

D. J. Nelson

Chairman, Radioecology Committee of the Ecological Society of America.

Chairman, The Third National Symposium on Radioecology.

Consultant, Advisory Committee on Reactor Safeguards.

Member-at-large, Board of Directors, American Society of Limnology and Oceanography.

Member, U.S. National Committee for the International Union for Quaternary Research, National Academy of Sciences, National Research Council.

Consultant, Mobile District, U.S. Army Corps of Engineers.

Lecturer in Zoology and Member of Graduate Faculty, University of Tennessee, Knoxville, Tennessee.

President, East Tennessee Chapter of the Health Physics Society.

J. S. Olson

Professor of Biology (part time), Department of Botany and Graduate Program in Ecology, University of Tennessee.

International Biological Program, Productivity of Terrestrial Ecosystems (IBP/PT) International Section. Interbiome coordination representative at Kevo, Finland, and Rome, Italy, September 1970; biome information meetings, Tjipayang, Indonesia, and Canberra, Australia, August 1971.

International Coordinator, Eastern Deciduous Forest Biome, US-International Biological Program.

Series Editor, *Ecological Studies, Analysis and Synthesis*, Springer-Verlag, Berlin-Heidelberg-New York.

Consulting Editor, *Encyclopedia of Science and Technology* (and Yearbook) McGraw-Hill, New York.

Study Committee for the Institute of Ecology (TIE), Ecological Society of America.

Adviser for Earth Day 1971, Oak Ridge High School and Students for Earth's Future.

Program Section Chairman, Ecosystem Analysis and Synthesis, Argonne National Laboratory, October 1970.

R. V. O'Neill

Member, U.S. International Biological Program Interbiome Modeling Committee.

Modeling Program Coordinator, U.S. International Biological Program, Eastern Deciduous Forest Biome.

Participant in Airlie Conference on Cybernetics and Large Systems, American Society for Cybernetics, February 1971.

D. E. Schile

Lecturer, University of Tennessee: Graduate Program in Ecology, and Department of Zoology and Entomology.

Member, Coordinating Committee, University of Tennessee Institute of Radiation Biology.

Member, Panel on General Ecology, Ecosystem Analysis, National Science Foundation.

Member, Environmental Quality Advisory Board of Oak Ridge, Tennessee.

Co-chairman, International Woodlands Coordinating Committee, International Biological Program.

Member, Oak Ridge Regional Planning Commission.

Editorial Board, *Ecological Monographs*.

Member, Executive Committee, Eastern Deciduous Forest Biome, Analysis of Ecosystem Program, U.S. IBP.

R. I. Van Hook

Participant, Institute of Ecology Study on Global Ecological Problems (June 1971), University of Wisconsin, Madison, Wisconsin. Resulting publication: *Man and the Living Environment*.

J. P. Witherspoon

Lecture course in "Radiation Ecology," Botany 6630 and 6640, Winter Quarter 1971, University of Tennessee, Knoxville, Tennessee.

Lab and field course in "Radiation Ecology," Botany 6650, Spring Quarter 1971, University of Tennessee, Knoxville, Tennessee.

Appointed as Lecturer in American Institute of Biological Sciences Radiation Biologists Program.

Participated in local and traveling lecture programs of the Cooperative Science Education Center, Oak Ridge, Tennessee.

M. Witkamp

Lecturer in Biology (part time), Department of Botany and Graduate Program in Ecology, University of Tennessee, Knoxville, Tennessee.

Guest Lecturer in Biology, Department of Biology, University of Puerto Rico, Rio Piedras, Puerto Rico.

IBP Process Coordinator for Terrestrial Decomposition, Eastern Deciduous Biome, U.S.A.

Woodland Representative, Microbiology Interbiome Coordinating Committee, Int. IBP.

Thesis Committee, Carol Macklin (Masters), Department of Biology, Emory University, Atlanta, Georgia.

Lecturer at Seminar, Microbial Contribution to Terrestrial Ecosystem Energy Flow and Nutrient Cycling, 71st Annual Meeting, American Society of Microbiology, Minneapolis, Minnesota.

Lecturer, Forest Leadership School, Symposium on Systems Ecology, Madison, Wisconsin.

Lecturer, Decomposer Conference, Athens, Georgia.

Ecological Sciences Division Publications

Reprints may be obtained by circling the desired numbers on the enclosed numbered sheet and mailing the sheet to:

Dr. Stanley I. Auerbach, Director
Ecological Sciences Division
Building 2001
Oak Ridge National Laboratory
P.O. Box X
Oak Ridge, Tennessee 37830

Publications marked by an asterisk are out of print -- none are available.

1. "A Modification of the Master-Charcoal Technique for the Rearing of Mites and Other Small Arthropods," by C. J. Rohde, Jr. *Ecology* 37(4), 843-44 (October 1956).
2. "Investigations on Sterility and Deformities of *Oonthophagus* (Coleoptera, Scarabaeidae) Induced by Gamma Radiation," by H. F. Howden. *Ann. Entomol. Soc. Amer.* 50(1), 1-9 (1957).
- *3. "Some Effects of Gamma Radiation on *Tropoderma sternale* Jayne," by H. F. Howden and S. I. Auerbach. *Ann. Entomol. Soc. Amer.* 51(1), 48-51 (January 1958).
- *4. *The Suspended Microbios of the Clinch River and Adjacent Waters, in Relation to Radioactivity in the Summer of 1956*, by J. B. Lackey. ORNL-2310 (August 1958).
- *5. *Need for Reserving Melton Valley for Long Range Ecological Studies*, by K. Z. Morgan and S. I. Auerbach. ORNL-CF-57-12-25 (1957).
- *6. "The Soil Ecosystem and Radioactive Waste Disposal to the Ground," by S. I. Auerbach. *Ecology* 39(3), 522-29 (July 1958).
7. "Concentration of Cesium-137 by Algae," by L. G. Williams and H. D. Swanson. *Science* 127(3291), 187-88 (1958).
8. "Effects of Gamma Radiation on Collembola Population Growth," by S. I. Auerbach, D. A. Cronley, Jr., and M. D. Engelman. *Science* 126(3274), 614 (September 1957).
- *9. "Strontium-90 and Cesium-137 Uptake by Vegetation Under Natural Conditions," by S. I. Auerbach and D. A. Cronley, Jr. *Proc. Intern. Conf. Peaceful Uses At. Energy, Geneva, 1958* 18, 494-99 (1958).
- *10. "Lethal Effects of Gamma Radiation upon Segments of a Natural Microbial Population," by R. J. Davis, V. L. Shelen, and S. I. Auerbach. *J. Bacteriol.* 72(4), 505-10 (October 1956).
- *11. "Uptake of Waste Sr-90 and Cs-137 by Soil and Vegetation," by E. R. Graham. *Soil. Sci.* 86(2), 91-97 (August 1958).
- *12. *Long-Range Ecological Study of the Oak Ridge Area: I. Observations on the Summer Birds of Melton Valley*, by J. C. Howell. ORNL-CF-58-6-14 (June 1958).
13. "Uptake of Cesium-137 by Cells and Detritus of *Euglena* and *Chlorella*," by L. G. Williams. *Limnol. Oceanogr.* 5(3), 301-11 (July 1960).
14. "A Sampling Device for Soil Microarthropods," by S. I. Auerbach and D. A. Cronley, Jr. *Acrologia* 8(3), 280-87 (1960).
15. "Long-Term Ecological Study in the Oak Ridge Area. III. The Oribatid Mite Fauna in Pine Litter," by D. A. Cronley, Jr., and K. K. Bohmack. *Ecology* 41(4), 785-90 (October 1960).
- *16. "Studies on the Biologies of Two Mite Species, Predator and Prey, Including Some Effects of Gamma Radiation on Selected Developmental Stages," by C. J. Rohde. *Ecology* 40(4), 572-79 (October 1959).
- *17. "Ecological Research," by S. I. Auerbach *et al.*, in *Health Phys. Div. Ann. Progr. Rept. July 31, 1957*. ORNL-2384, pp. 10-39.
- *18. "Ecological Research," by S. I. Auerbach *et al.*, in *Health Phys. Div. Ann. Progr. Rept. July 31, 1958*. ORNL-2590, pp. 27-52.
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