stratigraphies for this region throughout the time interval represented in the upland sites. In the lake cores, the tundra episode is only clearly recorded down to the top of highly inorganic sediments dated about 10,300 years B.P., although it is possible that longer lake cores would yield older tundra records. In contrast, the lower part of the marine stratigraphy registers the continuous presence of sedge-shrub-tundra vegetation to at least 21,000 years B.P. The fact that the total pollen concentration during this floral episode rarely falls below one-third of the modern values of 5000 grains per gram (dry weight) suggests the proximity of densely vegetated areas. Good evidence for a regional vegetation source of pollen is the persistently high amounts of Salix pollen at the marine site; this pollen type is not adapted for long-distance transport by air and is one of the least corrosion-resistant pollen types (18); hence, it is unlikely to survive reworking from older sediment. Thus there is strong evidence in the marine pollen stratigraphy to support the following hypothesis. Cartwright Saddle remained a seasonally open-water depositional environment during the Late Wisconsinan. Extensive areas of tundra vegetation were located within 100 km of the marine basin throughout this time, probably including much of the inner continental shelf above 100 m (present water depth) as well as the Labrador mainland nunatak and coastal refuges proposed by Ives (19).

Thus, foraminiferal evidence in the Cartwright Saddle sediment indicates open-water conditions during the past 22,000 years and the pollen spectrum indicates the continuous regional presence of terrestrial vegetation during this time. The almost exclusively arctic-subarctic foraminifera suggest that the open water was not due to the influx of warmer currents. Therefore, seasonal removal of the sea ice probably took place by processes similar to present-day conditions: that is, the ice cover broke in summer and was driven by winds toward the Atlantic. Lack of ice-rafted sediment in the cores precludes local melting. The fact that fast continental ice was not present in the basin suggests that the last glacial event in this region was not extensive.

The limit of the Wisconsinan ice along the northeast Canadian coast is controversial. An extended limit along the coast [for example, (20)] is disputed on the basis of field studies, which indicate that some of the coastal highlands on Baffin Island and Labrador were not overrun by the last episode of continental ice (21). Marine sediments contain SCIENCE, VOL. 202, 15 DECEMBER 1978

well-preserved evidence of glacial history, as demonstrated by the CLIMAP team (22) in the North Atlantic and our cores on the continental shelf. It is possible that sediments in small basins of the shelf contain the necessary information to settle the controversy of the Wisconsinan ice limits and to assist the work of CLIMAP by providing boundary information for paleoclimatic synthesis in the North Atlantic.

GUSTAVS VILKS

Atlantic Geoscience Centre, Geological Survey of Canada, Bedford Institute of Oceanography, Post Office Box 1006, Dartmouth, Nova Scotia

PETA J. MUDIE

Department of Geology, Dalhousie University, Halifax, Nova Scotia

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Carbon Flow in Four Lake Ecosystems: A Structural Approach

Abstract. Direct and indirect carbon fluxes in lakes Marion (British Columbia), Findley (Washington), Wingra (Wisconsin), and Mirror (New Hampshire) are compared, using budgets and input-output analysis. Overall differences in carbon flow between the lakes are shown with cycling indices of .031, .108, .572, and .661, respectively. The results suggest that lake ecosystems may be considered unique aggregations of similar components.

Lakes receive inputs from surface runoff, groundwater, and airborne materials. Their trophic status may fluctuate in response to changes in inputs of carbon and nutrients from their watershed due to disturbances such as those caused by logging, fertilization, or urbanization (1). These changes in carbon and nutrient input have traditionally been considered in terms of their effects on the primary trophic level-in particular on phytoplankton photosynthetic activity, planktonic community structure, and physiochemical factors influencing the biota. However, comprehensive analyses tracing inputs and subsequent metabolic effects throughout a lake ecosystem are rare (2). In this report we compare four such studies in an effort to evaluate differences in carbon cycling between

lakes. The purpose of this comparative analysis is to gain insights unavailable in site-specific research and to provide a basis for developing hypotheses concerning factors that regulate ecosystem structure.

The lakes included in this comparison are Findley Lake, an oligotrophic subalpine lake in the coniferous forest of the Cascade Mountains, Washington; Marion Lake, an oligotrophic lake on the mild wet Pacific coast of southern British Columbia; Mirror Lake, an oligotrophic lake surrounded by deciduous and coniferous forests in New Hampshire; and Lake Wingra, a marl-eutrophic lake receiving urban drainage in Madison, Wisconsin (Table 1). The lakes are similar in size, climate, and altitude, except Findley Lake, which is at a higher elevation

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Characteristic	Findley Lake	Marion Lake	Mirror Lake	Lake Wingra 43°03′N, 89°25′W			
Latitude and longitude	42°38′N, 121°22′W	49°17′N, 122°40′W	43°57′N, 71°42′W				
Elevation (m)	1,200	300	213	259			
Annual precipitation (cm)	270	240	120	77			
Basin area (ha)	129	13,000	85	1,556			
Geology	Lava flows, volcanic ash conglomerate	Glacial drift, hornblende, granitic	Metamorphosed granitic	Loess or till			
Original vegetation	Subalpine coniferous	Coastal coniferous (decid- uous fringe)	Deciduous coniferous	Prairie, deciduous			
Land use	Forest	Forest	Forest recreational	Urban forest plain			
Lake area (ha)	11.4	13.3	15.0	137.0			
Lake volume (m ³)	8.9×10^{5}	3.0×10^{5}	8.6×10^{5}	32.6×10^{5}			
Maximum depth (m)	27	6	11	6			
Percentage in littoral zone	~0	Moderate	Small	Large			
pH -	6.4	6.3-7.2	5.8-6.8	7.4-9.1			
Total alkalinity (mg/liter)	4-10	1-3	3-7	116-190			
Nitrate N (mg/m ³)	3-50	4-35	<2-70	<1-370			
Ammonia N (mg/m ³)	0-40		<10-50	10-900			
Phosphate P (mg/m ³)	<0.1-3	2-27	0.3-2	<1-20			
Renewal time (years)	0.14	0.015	1.0	0.48			

Table 1. Physical and chemical characteristics of the comparison lakes.

and has a commensurately shorter growing season. Chemical characteristics of the lakes vary widely as a function of the surrounding substrate geology, runoff characteristics, vegetation, and land-use patterns. The chemical and biological differences provide a gradient for comparative analysis.

The small-watershed approach to material cycling, in which carbon and nutrient budgets for ecosystems are calculated (3), provides a framework for comparing the patterns of elemental distribution, accrual, and loss in the lakes. For instance, carbon budgets reveal the amount of carbon entering a lake and the direct transfer from one trophic or abiotic component to the next. However, carbon budgets do not normally reveal the interdependence of these components, nor the amount of carbon recycled. To consider these features within a comparative framework we adapted the Leontief (4) input-output model, which has been used extensively in econometrics but rarely in ecology (5). The model is a mathematical statement that the total output of a system is composed of the flow out of the system plus some amount consumed internally in the process, which is assumed to be proportional to the total production. The carbon flux in an *n*-compartment ecosystem can be viewed in matrix form, the rows representing the sources and the columns the consumers of carbon (6). That is, each entry represents the carbon output p_{ii} of the row component *i* used by the column component *j* or lost to the system r_i (final demand) (Table 2). The total direct carbon flow e_i is the sum of internal consumption and outflows

$$e_i = \sum_j p_{ij} + r_i \tag{1}$$

The carbon flow of a component can be expressed as a linear function of the direct carbon flow of the consuming component

$$p_{ij} = g_{ij} e_j \tag{2}$$

where g_{ij} are the elements of the carbon matrix normalized by e_j . Substitution into Eq. 1 yields

$$e_i = \sum_j g_{ij} e_j + r_i \tag{3}$$

Restating Eq. 3 in matrix form and solving for e_i yields the structure matrix (Table 2)

$$\mathbf{E} = (\mathbf{I} - \mathbf{G})^{-1}\mathbf{R}$$
 (4)

where I is the identity matrix. The individual terms s_{ij} of $(I - G)^{-1}$ are the structural elements of the ecosystem, as **R** can be varied to produce changes in **E** without changing $(I - G)^{-1}$. Each element s_{ij} represents the total carbon flow, both direct and indirect (recycled), from the *i*th to the *j*th component per unit of final demand of the *j*th component, and hence represents the interdependence of the components. The magnitude of the cycled flow (E_c) is

$$E_{\rm c} = \sum_{i} e_i (s_{ii} - 1) / s_{ii}$$
 (5)

and the ratio of Ec to total system throughflow Σe_i) may be used to define a cycling index (7). This index indicates the fraction of carbon flow that is cycled. As such, it provides a convenient parameter for comparing ecosystems.

The production matrix (Table 2) represents a synthesis of data gathered for the individual projects, by methods described elsewhere (8-10). Briefly, Marion Lake has the largest total carbon inputs of all the lakes; the total carbon consisted of 86 percent dissolved inorganic carbon (DIC), 13 percent dissolved organic carbon (DOC), and 1 percent particulate organic carbon (POC). Of the POC inputs, 94 percent were allochthonous from fluvial sources and 6 percent were benthic primary production. Fluvial losses of DIC and DOC were comparable to their inputs, whereas POC losses were 43 percent of POC inputs. Respiration was primarily benthic. In Findley Lake, 59 percent of total carbon input was DIC, 34 percent was DOC, and 7 percent was POC. Of the POC inputs, 85 percent was fluvial. Of primary productivity, 67 percent was benthic. Fluvial losses and inputs of DOC were the same, whereas fluvial losses of DIC and POC were 84 and 40 percent of inputs, respectively. Lake Wingra inputs of carbon were also mostly DIC (82 percent), with 12 percent POC and only 6 percent DOC. Furthermore, primary production provided 91 percent of POC. Although macrophytes are present in Lake Wingra, their productivity is inhibited because of exclusion of light by the dense, shading populations of phytoplankton that constitute 77 percent of total primary production. Benthic respiration was only 53 percent of total respiration and was 44 percent of inflow DIC. The DOC fluvial losses were slightly greater than inputs, whereas the DIC losses were 67 percent of inputs and the POC losses only 2 percent of inputs. Because of hydrodynamic instability, resuspension of POC in Lake Wingra is a more or less continuous process. Mirror Lake inputs were more evenly divided, total carbon being 44 percent DIC, 33 percent DOC, and 23 percent POC. However, fluvial POC was only 11 percent of POC inputs, and plankton productivity dominated both POC inputs

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and system primary production. Inputs of DIC were only 48 percent of benthic respiration, DOC inputs and losses were comparable, DIC losses were 65 percent of inputs, and POC losses were 2 percent of inputs.

Comparison of the elements of the structure matrix reveals how the internal carbon structures of the lakes differ. Marion and Findley are similar in structure, although Marion has less interdependence of flows and Findley is without fish. In Marion Lake, the much greater flow of DIC supports the benthicrelated processes of insects, fish, and sediments. Furthermore, significant recycling occurs only in the insect and sediment sectors, which are comparable in their dependence on DIC and POC flow. The structure of Wingra and Mirror is quite different from that of Marion and Findley. In both lakes the interdependence of flows is much greater, being greatest in Mirror. The flow of DIC and POC required to support water column and benthic processes is much more uniform than in the two western lakes, with slightly more flow in the water column. More POC than DIC flows to support consumers and sediment processes in Wingra than in Mirror, where benthic flow is greater. Zooplankton flows are more important in Wingra than in Mirror, insect flow dominating in the latter.

The overall differences in direct and indirect carbon flow between lakes are

summed in the cycling index, which permits a clear ranking of the lakes. The cycling indices are .031 for Marion, .108 for Findley, .572 for Wingra, and .661 for Mirror, indicating increased cycling of carbon from Marion through Mirror.

Some of the factors regulating system structure are apparent. As with many other lakes, increasing primary production is proportional to nutrient loading (9). Higher inputs of allochthonous POC than of autochthonous POC favor insects over zooplankton (10). Increases in percentage and magnitude of autochthonous carbon sources result in progressively greater respiratory decomposition in the sediments (11). However, the total loading of carbon in these systems is not pro-

Table 2. Production (carbon budget) matrix, structure matrix, and cycling index (CI). For the carbon budget matrix values are grams of carbon per square meter per year; terms include DIC (dissolved inorganic carbon), POC (particulate organic carbon as detritus and phytoplankton), Zoo. (zooplankton), Ins. (benthic macroinvertebrates), Fish, Sed. (sediments, macrophytes, and periphyton), Outf. (outflow), Inf. (inflow, as precipitation, litter, and fluvial), PB (permanent burial), PA (pool addition), and PD (pool depletion) (error terms to balance the budgets). Each element p_{ij} represents the transfer from the row component *i* to the column component *j*; for instance, for Lake Wingra, $p_{23} = 52.2 = zooplankton$ consumption (ingestion) of POC. Dissolved organic carbon (DOC) budgets are not included in the calculations of total direct carbon flow or the structure matrix, as mechanisms for internal processing (if any) are not known. Each element of the structure matrix is the (direct and indirect) total carbon consumed by the row component *i* for the column component *j* per unit of final demand of component *j*; for instance, 1.90 g of carbon flows through DIC for every gram of carbon consumed by insects in Lake Wingra (s_{14}).

	Production matrix (P) (g m^{-2} year ⁻¹)											Structure matrix $(I - G)^{-1}$						
	Component carbon flow (p_{ij})							Final demand (r_i) Total		Structural elements (s_{ij})								
	DIC	POC	Zoo.	Ins.	Fish	Sed.	(DOC)	Outf.	PB	PA	(e_i)	DIC	POC	Z00.	Ins.	Fish	Sed.	
								Marion	Lake									
DIC		5.0				75.0		4692.8		35.5	4807.8	1.02	0.06	0.04	0.65	0.51	0.65	.031
POC	1.0		3.6			45.0		37.0			86.6	0.01	1.00	0.75	0.38	0.47	0.38	
Zoo.	4.0		1.4		0.6	0.2					6.2	0.00	0.00	1.29	0.06	0.30	0.00	
lns.	7.7				2.0	45.6		1.5			56.8	0.01	0.00	0.00	1.39	1.07	0.39	
Fish	1.3					0.6				0.7	2.6	0.00	0.00	0.00	0.01	1.00	0.01	
Sed.	101.8			56.7					8.0		166.5	0.03	0.00	0.00	1.40	1.08	1.40	
Inf.	4692.0	81.0					(708)				4773.0							
PD		0.6	1.2	0.1		0.1					2.0							
(DOC)								(710)										
								Findley	Lake									
DIC		2.5				5.0		983	LUKE	20.3	126-1	1 02	0.16	0.16	0.56	0.00	0.56	100
POC	0.5	2.0	22			5.0		6.6		1 2	16.2	1.05	1.01	1.01	0.50	0.00	0.30	.108
Z00	2.0		0.3			0.1		0.0		1.5	10.5	0.03	1.01	1.01	0.30	0.00	0.30	
Ins	1 2		0.5			0.1		0.2		0.1	2.5	0.02	0.00	1.14	0.02	0.00	0.02	
Fish	1.2					9.4		0.5		0.0	11./	0.05	0.01	0.01	1.90	0.00	0.90	
Sed	48			117					2.0	07	20.2	0.00	0.00	0.00	0.00	1.00	0.00	
Inf	117.6	13.8		11./			(69)		5.0	0.7	121.4	0.09	0.01	0.01	1.92	0.00	1.92	
PD	117.0	15.0					(00)				151.4							
(DOC)								(67)										
								Taba W	•									
DIC		420.0				170.0		Lake WI	ingra		000 0	• • •						
POC	150.0	430.0	52.2			1/0.0 5(0.0		203.0			803.0	2.02	1.86	1.70	1.90	1.72	1.90	.572
700	10.0		21.2			360.0		10.0		31.8	804.0	1.40	2.75	2.52	2.44	2.51	2.44	
ZUU. Inc	40.0		21.3		0.0	2.5		0.6			78.4	0.19	0.18	1.53	0.18	1.42	0.18	
IIIS. Eich	5.0				0.6	28.7		0.6			36.7	0.06	0.08	0.07	1.11	0.16	0.11	
FISH	225.0	220.0		267		1.5				2.2	7.2	0.01	0.01	0.01	0.01	1.01	0.01	
Jeu.	233.0	330.0		30.7					110.0	51.0	762.7	1.28	1.75	1.60	2.67	1.69	2.67	
IIII.	501.0	44.0	4.0				(20)				345.0							
	60.5		4.9					(2 1)			65.4							
(DUC)								(24)										
								Mirror 1	Lake									
DIC		56.0				5.0		8.6		9.8	79.4	2.91	2.40	2.38	2.21	2.27	2.21	.661
POC	19.1		12.8			35.0		1.0			67.9	2.15	2.77	2.75	2.41	2.54	2.41	
Z00.	12.0		5.2		0.5	0.4					18.1	0.65	0.54	1.93	0.51	1.06	0.51	
Ins.	6.8				0.8	40.2		1.3		0.9	50.0	1.40	1.16	1.15	2.96	2.26	1.96	
Fish	0.6					0.3				0.4	1.3	0.03	0.03	0.02	0.03	1.03	0.03	
Sed.	27.6		-	50.0					8.0		85.6	2.41	1.99	1.98	3.72	3.05	3.72	
Inf.	13.3	7.0				4.7	(10)				20.3					2.00	22	
(DOC)		4.9	0.1					(9)			9.7							

portional to the actual utilization patterns of carbon throughout the system. For example, the loading of DOC to lakes can be many orders of magnitude higher than that of POC, and its demands on the respiratory capacity of the ecosystem are virtually unknown. A simple linear correlation between the retention period and cycling index $(r^2 = .86,$ where r is the correlation coefficient) suggests the overriding influence of flushing rate on the structure of the lake.

These results support the concept that lake ecosystems may be considered as unique aggregations of similar components. The individual linkages-for instance, of nutrients and producers or predators and prey-operate within a certain range in all lakes (although the factors actually determining the couples are complex). Lakes differ in the relative combination of these similar structural elements as one factor or another is selectively enhanced, according to the nature of the inputs, lake morphometry, or flushing rate.



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Ozone Formation Related to Power Plant Emissions

Abstract. A curious and unambiguous event of excess ozone formation downwind of a power plant has been analyzed. A kinetic model used to simulate the event indicates that the excess ozone can be reconciled entirely on the basis of excess nitrogen oxides in the polluted air.

The chemistry of emissions from electricity-generating plants that use fossil fuels has become an important and controversial subject. One aspect of the controversy involves "O3 bulges," a phenomenon first reported by Davis et al. (1). According to their report, O₃ concentrations in the domain of aged yet well-defined plumes sometimes exceeds the concentrations in the ambient air. The finding was in contrast to all other monitoring data that had shown the expected trend of O₃ depletion in the paths of power plant plumes. More recent studies gave mixed results. No evidence of O_3 bulges was found in studies conducted in



Fig. 1. Aerometric data showing the concentrations of SO₂, particles larger than 0.01 μ m, and O_3 in a power plant plume traveling 300 m above Lake Michigan.