Reports

Carbon-13 Depletion in a Subalpine Lake: Carbon Flow Implications

Abstract. *Plankton (larger than 76 micrometers) taken from an undisturbed oligotrophic lake was found to have $\delta^{13}C$ values ($= {}^{13}C/{}^{12}C$ relative to the Pee Dee belemnite standard) ranging from −44 to −47 per mil. This extraordinary ${}^{13}C$ depletion, together with characteristics of the inorganic carbon pool, indicates that lake respiration as well as surrounding soil respiration provide important carbon sources for plankton production in this lake.*

Research in 1976 on the use of ${}^{13}C$ as a naturally occurring carbon tracer in the Findley Lake watershed (*1*) revealed that plankton, taken from a vertical haul (lake bottom to surface) of a plankton net (76-μm mesh), had a $\delta^{13}C$ value of −45 per mil (*2*). Subsequent sampling and analysis during the following year confirmed that this carbon pool, composed almost entirely of zooplankters *Chaoborus* sp. and *Diaptomus* spp., had consistently lower $\delta^{13}C$ values (Fig. 1) than all naturally occurring plankton and most organic carbon heretofore reported (*3*). One feature of the carbon flow in this soft-water lake immediately came into question: Was the movement of carbon from air to this freshwater pelagic food chain as direct as the case described by Schindler *et al.* (*4*)?

As reviewed by several investigators (*5*), atmospheric CO_2 ($\delta^{13}C \doteq -7$ per mil) is used by plants to produce organic carbon whose $\delta^{13}C$ ranges from −10 to −30 per mil. In light of these investigations, it was not possible that the low concentrations of ${}^{13}C$ in Findley Lake plankton were the result of a one-step isotope fractionation of atmospheric CO_2 by aquatic plants. Nor was it likely that pelagic consumers, the bulk of the plankton collected, were themselves significantly altering the ${}^{13}C/{}^{12}C$ ratio from that of their food source (*6*). A more plausible explanation would be that biogenic (respiration) CO_2, depleted in ${}^{13}C$, was an important component of the inorganic carbon used to produce the organic material in question. Inorganic $\delta^{13}C$ lowered by the addition of biogenic CO_2 has been found in a variety of environments (*7*).

The dissolved inorganic carbon (DIC) at several depths in the lake was analyzed (*8*) and found to have $\delta^{13}C$ values consistently below that of atmospheric CO_2 (Fig. 1). The $\delta^{13}C$ (DIC) values decreased with depth to lows of −20 to −22 per mil at 25 m, whereas the DIC concentrations increased with depth to maxima of 6 to 9 mg/liter (Fig. 1). These features were present under both winter and summer thermal stratification. Moreover, little change in DIC concentrations occurred diurnally during the peak period of algal production. Lack of diurnal change in DIC concentrations indicated that water-column photosynthesis and respiration processes must be small relative to the DIC pool and must have little influence on it. Indeed, the maximum phytoplankton uptake of DIC in this lake, 800 mg m^{-2} day^{-1} (*9*), represents less than 1 percent of the 10^5 mg of DIC per square meter present in the photic zone. Plankton respiration was shown to be an even smaller quantity (*10*).

The above results suggest that nonpelagic biological processes must be affecting the size of the lake's DIC pool and its isotope characteristics. If one compares under-ice to post-ice-out conditions, it is evident that considerable buildup of DIC occurred during the winter. Dissolved oxygen concentrations in deep lake water were inversely related to DIC concentrations, an indication that lake (probably benthic) respiration was indeed generating some of the inorganic carbon present. As noted by Rich and Devol (*11*), however, the ratio of CO_2 production to O_2 uptake in the water column ranges from 2.7 to 5.2 and they conclude that "a very oxidized product is entering the lake, or a reduced product is leaving, in significant amounts."

The $\delta^{13}C$ of soil water DIC sampled from several soil depths near the lake in June 1977 ranged from −22 to −25 per mil, somewhat lower than that of hypolimnetic water. With a lake water renewal time of about 2 months and with a

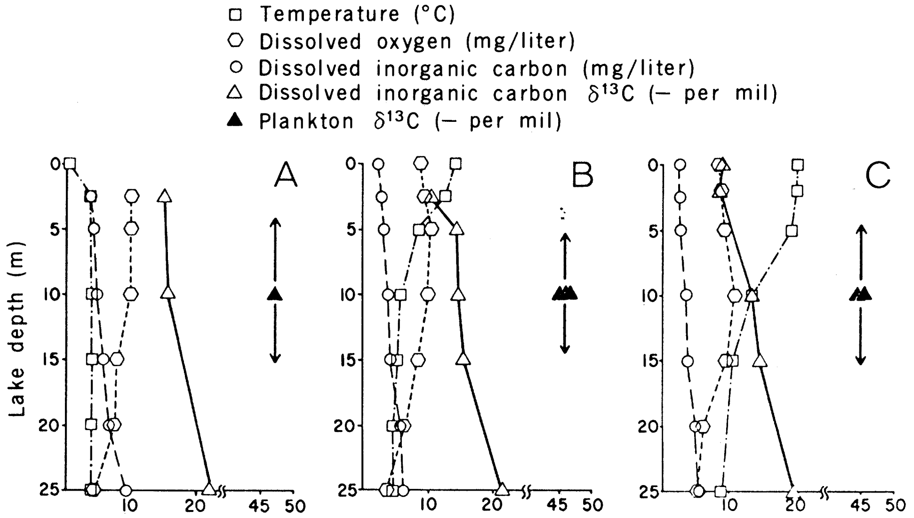

Fig. 1. Depth profiles of water temperature, dissolved oxygen concentrations, dissolved inorganic carbon concentrations, and dissolved inorganic carbon $\delta^{13}C$ under ice (A), 15 to 20 days after ice-out (B), and 60 to 70 days after ice-out (C). The $\delta^{13}C$ of the total water column plankton (> 76 μm) is also shown. In using the same ordinate scale for all measurements, I have plotted the $\delta^{13}C$ values without their minus signs. The 95 percent confidence limits for each $\delta^{13}C$ treatment were < ± 1 per mil. Concentration data are from unpublished Coniferous Forest Biome research.

Scoreboard for Reports. The acceptance rate for Reports during the last year has been about 25 percent. The number accepted has exceeded the number published and publication delay has increased to about 4 months. For the next few months, our acceptance rate will be about 15 percent, or 10 Reports per week.

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sizable portion of this water probably supplied by subsurface runoff (*12*), allochthonous DIC could be an important carbon source for the lake. During the spring snowmelt, temporary surface streams flowing into Findley Lake had $\delta^{13}C$ (DIC) values of −18 per mil. Thus the inorganic carbon species CO_2 (gaseous), CO_2 (aqueous), and HCO_3^- originating from soil respiration and entering the lake by way of surface water and groundwater may be the oxidized products suspected by Rich and Devol (*11*). Soil respiration, as measured by the evolution of CO_2 from the nearby forest floor, varied from 0.6 to 3.6 g of carbon per square meter per day during a 1-year investigation (*13*). This rate of production of inorganic carbon in the surrounding soil is greater by some two orders of magnitude than that reported to occur in the lake (*10*).

The $\delta^{13}C$ of respiration CO_2 under aerobic conditions should be about equal to that of the organic substrate metabolized (*14*). The $\delta^{13}C$ of both soil (−26 to −29 per mil) and lake sediments (−28 to −33 per mil), however, was consistently lower than the $\delta^{13}C$ values of associated DIC. A similar situation in several eastern United States lakes was also found by Oana and Deevey (*7*). They cited the addition of carbon from the atmosphere, lithologic carbonate, and fermentation CO_2 as causing the elevated $\delta^{13}C$ (DIC) values. Dissolution of carbonate cannot be important in Findley Lake because the parent material of the watershed is entirely of volcanic origin (*15*). It is not known how significant deep sediment anaerobiosis may be since profundal waters are usually well oxygenated and surface sediments generally exhibit positive values of *Eh* (oxidation-reduction potential) (*10*). Carbon-13 enrichment of DIC in shallower water undoubtedly represents the addition of atmospheric CO_2. Epilimnetic ^{13}C enrichment progresses after ice-out (Fig. 1), suggesting that the 8-month ice cover inhibits atmospheric CO_2 invasion into the lake during this time.

Coupled with the inverse relationship between $\delta^{13}C$ (DIC) and water depth is evidence that the maximum photosynthetic uptake of DIC in the lake occurs below 10 m (*9*). This deep-water photosynthesis increases the likelihood that ^{13}C-depleted DIC is used for phytoplankton production. If DIC at 10 m (−15 per mil) is the primary inorganic carbon source for algae during the major production period (0 to 30 days after ice-out), this leaves roughly a difference of 30 per mil between the DIC and plankton $\delta^{13}C$. A fractionation of 28 per mil has been reported for a marine *Cyclotella* incubated at 10°C. Species of this genus comprise a sizable portion of the phytoplankton in Findley Lake (*9*).

There has been considerable speculation on the importance of terrestrial detritus as an organic carbon base for the pelagic food chain in this (*10*) and other mountain lakes (*16*). Since the predominant land plant biomass in the Findley Lake watershed has $\delta^{13}C$ values of −25 to −29 per mil, it is unlikely that this material could provide a food base for zooplankton with a $\delta^{13}C$ of −45 per mil, unless an unexpectedly large heterotrophic isotope fractionation was occurring. Terrestrial detritus must compose most of the organic carbon pool of the benthos, however, as shown by sedimentation studies (*17*) and the $\delta^{13}C$ of surface sediments. Annual benthic respiration in this lake has been reported to exceed the sedimentation of lake-produced organic carbon by a factor of 3 (*10*), thus implicating the metabolism of allochthonous substrates as a source of DIC. Whatever the organic material, its degradation in lake sediments and surrounding soil releases ^{13}C-depleted CO_2, which, in combination with atmospheric and perhaps fermentation CO_2, forms the DIC available for phytoplankton production. Algal isotope fractionation of this inorganic carbon together with possible although probably small heterotrophic fractionation effects very likely are responsible for the low $\delta^{13}C$ of Findley Lake plankton.

In conclusion, although atmospheric CO_2 must be the initial carbon source for all organic carbon production in this watershed, much of the DIC available for deep and seasonally early phytoplankton production in Findley Lake has been previously reduced and oxidized. This carbon flow is indicated by the ^{13}C-depleted nature of the lake's DIC and plankton carbon. Nonpelagic sites must participate in both the fixation and respiration processes that precede carbon "refixation" in the lake. In view of the large number of similar lake and watershed environments in the Cascade Mountain range (*18*), these conditions are probably not exceptional. The resulting dissimilarity between $\delta^{13}C$ in plankton and that in land plant material may provide a much needed tool for determining the importance and fate of both carbon sources in these lake systems.

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References and Notes

1. Findley Lake is located at an elevation of 1128 m near the crest of the Cascade Mountain range some 70 km southeast of Seattle. Much of the 104-ha undisturbed watershed is forested with a mixture of Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*). The lake has a surface area of 11.4 ha, a maximum depth of 28 m, and a mean depth of 8 m. Low nutrient concentrations and carbon fixation rates prevail. See (*10*) for further details.
2. $\delta^{13}C = \{[(^{13}C/^{12}C)_{\text{sample}}/(^{13}C/^{12}C)_{\text{PDB}}] - 1\} \times 10^3$ per mil, where PDB is the Pee Dee belemnite standard. I analyzed dried samples by oxidizing the organic carbon of the material to CO_2 using the break-seal combustion method of D. L. Buchanan and B. J. Corcoran [*Anal. Chem.* **31**, 1635 (1959)]. The gases from a combusted sample were passed over metallic Ag and Cu at 400°C, and Dry Ice–ethanol-cooled glass to remove respectively, halogens, NO_x, and H_2O. Thus purified, the CO_2 was then frozen into a sample tube at liquid-nitrogen temperature and transferred to a Nuclide 6-60 ratio mass spectrometer for analysis. The 95 percent confidence limits for the means of all $\delta^{13}C$ treatments was $< \pm 1$ per mil.
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6. Small differences in $\delta^{13}C$ observed between phytoplankton and associated zooplankton are cited by P. M. Williams and L. I. Gordon [*Deep-Sea Res.* **17**, 19 (1970)].
7. For example: air, C. D. Keeling, *Geochim. Cosmochim. Acta* **13**, 322 (1958); lakes, S. Oana and E. S. Deevey, *Am. J. Sci.* **285-A**, 253 (1960); soils, E. M. Galimov, *Geochem. Int.* **3**, 889 (1966); sea, W. G. Deuser and J. M. Hunt, *Deep-Sea Res.* **16**, 221 (1969); fresh and brackish water, W. G. Mook, in *Proceedings, Isotope Hydrology* (International Atomic Energy Agency, Vienna, 1970), pp. 163–190.
8. The DIC of water samples taken from various lake depths was removed by acidification with phosphoric acid to $pH < 4$ and purging with N_2 gas while the sample was heated and magnetically stirred for 1.5 hours. The resultant CO_2 was collected and analyzed as was the CO_2 from organic samples (*2*).
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19. I thank Dr. M. Stuiver; associates Drs. A. Yang, P. Grootes, and P. Quay; and B. Burk, P. Wilkinson, P. Reimer, and J. McCracken, all of the Quaternary Research Center, University of Washington, for their generous assistance. The support of Drs. R. Gara and R. Wissmar, also of the University of Washington, is gratefully acknowledged. I express special thanks to Dr. F. Ugolini and J. Zachara for providing soil water samples. This work was funded by NSF grant DEB74-20744-A06 to the Coniferous Forest Biome, Ecosystem Analysis Studies. This is contribution No. 321 from the Coniferous Forest Biome.

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