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Authors
Williams, PM
Smith, KL
Druffel, EM
et al.

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Dietary carbon sources of mussels and tubeworms from Galapagos hydrothermal vents determined from tissue ^{14}C activity

P. M. Williams*, K. L. Smith*, E. M. Druffel† & T. W. Linick†

* Scripps Institution of Oceanography and
† Department of Chemistry, University of California, San Diego, La Jolla, California 92093, USA

The large quantities of reduced carbon that are required to support the filter-feeding mytilid mussels (*Mytilus* sp.), vesicomyid clams (*Calyptogena* sp.) and various other animals in the Galápagos hydrothermal vent systems are thought to be derived from either the *in situ* synthesis of particulate organic matter by chemoautotrophic, sulphide-oxidizing bacteria[1,2] or by the advection of sedimentary organic carbon into the vent environment from surrounding areas[3,4]. In contrast, the dense populations of vestimentiferan tubeworms (*Riftia pachyptila*), which lack mouth organs and digestive tracts, apparently utilize organic carbon synthesized by symbiotic chemoautotrophs[5]. We present evidence here, based on ^{14}C activities and $^{13}C/^{12}C$ ratios, that the principal source of dietary carbon for mussels and tubeworms is derived from the dissolved inorganic carbon (DIOC) in the vent effluent waters.

There are two postulated sources of particulate organic carbon (POC) available as dietary carbon to filter-feeding organisms. The first is sedimentary POC derived from DIOC fixed photosynthetically at the ocean's surface which subsequently reaches the ocean floor. Its radiocarbon activity is assumed to be the same as that of the DIOC in surface water ($+20 \pm 20$, Table 1). The $\delta^{13}C$ of this POC (-22, Table 1) is a mean value derived from $\delta^{13}C$ measurements of POC[6,7] collected below 500 m. The second source is POC synthesized chemoautotrophically from DIOC in the vent waters. This DIOC originates from both magmatic activity[8] ($\Delta^{14}C = -1{,}000$ or 'dead' carbon) and the ambient bottom water ($\Delta^{14}C = -233$, Table 1) which mixes with the high-temperature hydrothermal fluid. As the organic ^{14}C activities of the organisms grown in the vent systems reflect the $\Delta^{14}C$ of these three carbon sources and the $^{13}C/^{12}C$ ratios reflect the carbon isotope fractionation occurring during synthesis of organic tissues in these organisms, it is possible to calculate the relative contribution of each carbon source using the following equations:

$$\Delta^{14}C_{mussel} = x(-1{,}000) + y(-233) + z(20) \quad (1)$$

$$\delta^{13}C_{mussel} = (x + y)(\delta^{13}C_{vent\ POC}) + z(-22) \quad (2)$$

where x, y and z are the relative amounts of magmatic DIOC, ambient DIOC and sedimentary POC, respectively. The $\delta^{13}C$ of POC in the vent water is unknown. Both of the above equations have to be satisfied to determine the relative amounts of the three possible dietary carbon sources utilized by the filter-feeding organisms.

The quantitative contribution of sedimenting POC to the food supply for filter-feeding vent organisms is questionable considering the flux of POC to the ocean floor and the *in situ* respiration rates of mussels. The total, mean flux of POC to the sea floor at 2,670 m 0°35.75′ N, 86°05.66′ W measured 20 and 100 m above the bottom on 4 July 1976 was 2.0 g C $m^{-2}yr^{-1}$ (ref. 9). *In situ* measurements of individual mussel respiration rates by K. Smith (unpublished results) range from 0.30 to 0.81 ml O_2 h^{-1} in dense mussel beds. Assuming a respiratory quotient of 0.85, then these rates are equivalent to an organic carbon requirement of 1.2–3.3 g C yr^{-1} (mean = 2.3 g C yr^{-1}). Thus, each mussel would essentially require the total annual POC flux per square metre for maintenance with no growth.

The ^{14}C activity of the mussel tissue could result from a mixture of sedimentary POC and POC of low ^{14}C activity derived from DIOC in the vent waters. The maximum amount of magmatic DIOC in the Galápagos vent waters ($T = 17$ °C) has been estimated to be 375 μmol kg^{-1}, a 13% increase above the ambient DIOC concentration of ~2,400 μmol kg^{-1} (refs 10, 11). If 13% of the vent water DIOC is magmatic ($\Delta^{14}C = -1{,}000$) and the remaining 87% is composed of ambient DIOC ($\Delta^{14}C = -233$) plus sedimentary POC derived from the DIOC in surface water ($\Delta^{14}C = +20$), then the maximum amount of sedimentary POC that could be incorporated into mussel tissue ($\Delta^{14}C = -267$) is 26% (equation 1). Estimates of mussel density in the 'Musselbed' vent area (W. Smithy, personal communication) are 20 ± 9 specimens per 0.25 m^2 in the immediate vicinity of the vent plume. If the mussels are utilizing the calculated maximum of 26% of sedimentary POC for growth (taken here as equivalent to maintenance), then each vent musselbed would use ~48 g C $m^{-2}yr^{-1}$ (0.26×2.3 g C yr^{-1} per mussel $\times$ 80 mussels per m^2), or about 35% of the annual primary productivity per square metre in the euphotic zone[9] for the growth of mussels alone.

There is a significant difference between the $^{13}C/^{12}C$ ratios, as well as ^{14}C activities, of mussel tissue collected 1 and 8 m from the vent plume (Table 1). If sedimentary POC ($\delta^{13}C = -22$) was incorporated into the tissue of the 8-m mussel, the resulting $\delta^{13}C$ value (-32.3) would be less than that observed (-32.8). This calculation assumes that the ^{14}C activity of the 8-m mussel tissue ($\Delta^{14}C = -228$) is derived from a mixture of 14% sedimentary POC ($\Delta^{14}C = +20$) and 86% chemosynthetic POC ($\Delta^{14}C = -267$) (equation 1).

If the ^{14}C activity of mussel shell carbonate reflects the ^{14}C activity of DIOC in the surrounding seawater, then the 21‰ decrease in $\Delta^{14}C$ between the ambient seawater DIOC and the mussel shell carbonate reflects dilution of the ambient DIOC with 3% magmatic DIOC. For the two clam shell carbonates, the 30‰ decrease in $\Delta^{14}C$ would represent dilution of the ambient DIOC with 4% magmatic DIOC, taking the ^{14}C activity of the bottom water at 21° N to be the same as at the Galapagos rift zone. A similar calculation gives 4.4% magmatic DIOC incorporated into cellular carbon synthesized by the chemoautotrophic bacteria and used by the mussels 1 m from the plume (provided the contribution from sedimentary POC is negligible).

The identical ^{14}C activities of the vestimentiferan tubeworm tissue and the mussel tissues collected 1 m from the vents strongly suggest that the tubeworms and mussels are utilizing the same DIOC sources, even though $\delta^{13}C$ in the tubeworm tissue is 23‰ greater than in the mussel tissue (Table 1). These atypical $^{13}C/^{12}C$ ratios found in the vent organisms have been discussed by Rau[12,13]. If bacterial chemosynthesis is the major process providing dietary carbon for the mussels and tubeworms, it is still unclear why carbon isotope fractionation should be different between chemoautotrophic synthesis occurring in the vent waters and internally (symbiotically) in the tubeworms.

An additional carbon source which may contribute to the bacterial synthesis of POC in the vent waters is methane, energetically a more favourable substrate for the growth of heterotrophic bacteria than DIOC. Methane concentrations up to 3.4 μmol kg^{-1} have been measured in the Galápagos vent

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Table 1 $\Delta^{14}C$ and $\delta^{13}C$ values of Galápagos vent organisms and relevant carbon sources

Sample description	(‰) $\Delta^{14}C$	(‰) $\delta^{13}C$	Ref.
Mussel tissue—dive 880 ('Musselbed', 1 m from vent)	−270±6	−33.9	This work
Mussel tissue—dive 895 ('Musselbed', 1 m from vent)	−263±8	−33.8	This work
Mussel tissue—dive 880 ('Musselbed', 8 m from vent)	−228±12	−32.8	This work
Mussel shell—dive 991 ('Musselbed', 1 m from vent)	−254±6	+2.8	This work
Tubeworm tissue—dive 993 ('Garden of Eden', in vent plume)	−270±20	−10.9	This work
Clam shell—dive 981 (East Pacific Rise, 21° N)	−263±6	+3.1	This work
Mussel tissue ('Clambake I specimen, 8 replicates)	—	−32.7 to −33.6	12
Tubeworm tissues ('Rose Garden')	—	−10.8 to −11.0	13
Clam shell ('Clambake I')	−263±10	—	10
Total DIOC, 2584 m* (Geosecs Station 337)	−233.4	—	14
Total DIOC, surface sea water	+20±20	−1.7 to −3.5	15
Particulate organic detritus >500 m	—	−20 to −25; mean −22	6, 7

The three mussels for tissue analysis were collected 1 and 8 m from the 'Musselbed' vent plume, *Alvin* dives 880 (21 January 1979) and 895 (20 February 1979), 0°47.89′ N, 86°09.21′ W at 2,493 and 2,480 m. The mussel for shell analysis was collected 1 m from the 'Musselbed' vent plume, *Alvin* dive 991 (8 December 1979) at 2,490 m. The tubeworm was collected in the 'Garden of Eden' vent plume, *Alvin* dive 993 (10 December 1979), 0°47.69′ N, 86°07.74′ W at 2,518 m. The clam for shell analysis was collected from the East Pacific Rise hydrothermal vent system, *Alvin* dive 981 (5 November 1979), 20°50′ N, 109°06′ W at ~2,600 m. The mussel tissue and tubeworm specimens were frozen after collection, and the tissue and shell samples rinsed with $^{14}CO_2$-free, organic carbon-free distilled water before drying. To determine ‰$\Delta^{14}C$ and ‰$\delta^{13}C$, all samples but the tubeworm tissue were burned in O_2 or acidified with HCl to give CO_2 which was converted to acetylene, via lithium carbide[15] and then counted for 2 days in each of two stainless-steel 1.0-l and 0.4-l gas proportional counters. The worm tissue CO_2 was purified by absorption onto CaO, diluted with background gas and counted twice in a 200-ml copper proportional counter for a total of 12 days. All countings were corrected for isotope fractionation (to a standard value of $\delta^{13}C = -25.0$‰ PDB-1) and for decay since the time of formation (to AD 1950). The standard was 95% of the net National Bureau of Standards oxalic acid count rate, corrected to a $\delta^{13}C = -19.0$‰, and the results are reported in terms of $\Delta^{14}C$ ($\pm 1\ \sigma$ counting error) which is the per million (‰) deviation from the ^{14}C activity of nineteenth-century wood[16]. The $^{13}C/^{12}C$ ratios are reported as $\delta^{13}C$ (±0.2‰) relative to the PDB-1 standard.

* The $\Delta^{14}C$ of the 2,490-m bottom water at the 'Musselbed' was assumed to be identical to the $\Delta^{14}C$ in 2,584-m water at Geosecs station 337, 24 May, 1974, 04°50′ N, 124°05′ W. σ_T at 2,500 m at both locations is 27.76±0.01 (ref. 17).

† $\Delta^{14}C$ values taken from corals collected from 3–5-m depth at 1.5° S, 90–91° W, assuming the $Ca^{14}CO_3$ reflects the ^{14}C activity of the surface seawater DIOC.

waters (M. D. Lilly, M. A. de Angelis and L. I. Gordon, unpublished results), and it has been calculated that 50 μmol kg^{-1} of abiogenic CH_4 of magmatic origin could be present in the 'end member' 350 °C hydrothermal fluid at the East Pacific Rise[18]. If methane were the sole carbon source for the synthesis of POC utilized by the mussels, then the mussel tissue would contain no measurable radiocarbon activity. Obviously this is not the case. It is possible that the ^{14}C activity of the mussel tissues (−267) is 13‰ lower than that of the mussel shell carbonate (−254) due to mussels taking up both 'dead' CH_4 and DIOC, whereas the shell is only using 'dead' DIOC.

On the basis of the ^{14}C activities and $^{13}C/^{12}C$ ratios reported here, we conclude that: (1) filter-feeding organisms in the vent system are directly or indirectly incorporating 'dead' carbon of magmatic origin into their tissue; (2) ~25% or less of the dietary carbon available to the mussels is from sedimenting POC fixed photosynthetically at the surface; and (3) mussel tissue is incorporating relatively more 'dead' DIOC than is mussel shell carbonate in specimens collected at the same location near the vent.

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A natural biological control of Dutch elm disease

Joan Webber

Department of Botany and Microbiology, University College of Wales, Aberystwyth SY23 3DA, Dyfed, UK

Since its arrival in the late 1960s, the aggressive strain of *Ceratocystis ulmi*, the fungus that causes Dutch elm disease, has destroyed over 20 million elms in Britain and subsequently inflicted similar heavy losses across much of continental Europe[1,2]. Successful control of the disease has been achieved only locally, using intensive sanitation and fungicide injection programmes[3,4]. However, it has recently become apparent that disease spread may also be limited naturally. I present here evidence of a biological control of Dutch elm disease which could be exerting an important effect in some parts of Britain. This control process acts by preventing successful breeding of scolytid beetles which are the vectors of *C. ulmi*.

The control phenomenon was first encountered during 1976 and 1977 in several stands of trees in mid and south Wales. Each stand contained between 10 and 100 wych elms (*Ulmus glabra*) and although *C. ulmi* had killed some trees in all these stands, disease spread to healthy trees was surprisingly slow, suggesting that only small numbers of beetle vectors were present. Investigation of beetle breeding material, that is, the inner bark of dying or recently dead trees, revealed only a limited amount of active breeding. Instead such bark commonly exhibited dark zone lines (Fig. 1*a*), which on isolation yielded the fungus

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