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Contribution of dissolved organic C to stream metabolism: a mesocosm study using ^{13}C-enriched tree-tissue leachate

TRACY N. WIEGNER[1], LOUIS A. KAPLAN[2], AND J. DENIS NEWBOLD[3]
Stroud Water Research Center, 970 Spencer Road, Avondale, Pennsylvania 19311 USA

PEGGY H. OSTROM[4]
206 Natural Science Building, Department of Geological Sciences, Michigan State University, East Lansing, Michigan 48824-1115 USA

Abstract. Dissolved organic C (DOC) is metabolically important in streams, but its contribution to ecosystem metabolism is not well known because it is a complex mixture of mostly unidentified molecules. The uptake of bioavailable DOC in White Clay Creek (WCC), a 3rd-order stream in Pennsylvania, was estimated from the results of an experiment using ^{13}C-labeled tree-tissue leachate and streambed sediments in recirculating mesocosms. The contribution of DOC in transport to stream metabolism was estimated from measurements of ^{13}C-DOC uptake, ^{12}C-DOC concentrations, and diel changes in dissolved O_2 in the mesocosms. Eighty percent (±5) of the DOC in the ^{13}C-tree-tissue leachate was bioavailable and belonged to 1 of 2 distinct lability classes, readily and intermediately labile. These components made up 88% (±0.6) and 12% (±0.6), respectively, of the biodegradable DOC in the leachate. Uptake mass transfer coefficients for the readily and intermediately labile components were 55 (±24) μm/s and 2.6 (±0.13) μm/s, respectively. Based on our mesocosm measurements, DOC in transport could support 33 to 54% of the bacterial C demand and up to 51% of the community respiration in WCC. Extrapolation of our results to WCC indicates that readily and intermediately labile DOC similar in quality to the ^{13}C-DOC would travel 175 and 3692 m downstream in WCC before being taken up by the sediments. These distances represent ~7% and >150% of the length of the 3rd-order reach. Our results suggest that readily labile DOC is an important energy source at the reach scale, whereas intermediately labile DOC serves as an energy subsidy from upstream to downstream reaches.

Key words: carbon-13, dissolved organic carbon, ecosystem metabolism, leachate, stable isotopes, tracers, streams.

Dissolved organic matter (DOM) plays an important metabolic role in streams and rivers by supplying energy and C to heterotrophic bacteria (Meyer et al. 1988). The incorporation of dissolved organic C (DOC) into the microbial food web affects the amount and rate at which DOC is supplied to higher trophic levels. DOC stimulates both pelagic and benthic bacteria in running waters (e.g., Bott et al. 1984, Servais et al. 1987, Volk et al. 1997). The primary site for DOM use and bacterial activity in low-order streams is in the benthic sediments (Lock and Hynes 1976, Dahm 1981, Fischer and Pusch 2001, Fischer et al. 2002b). However, the relative contribution of DOC from the water column to stream and riverine metabolism is not well known, in part because DOC is a complex mixture of mostly unidentified molecules from various sources with varying labilities (Thurman 1985, Fischer et al. 2002a). In addition, in situ measurements of DOC use in stream water are complicated by processes that continually produce, transform, and consume DOC molecules in transport. Thus, a tracer with characteristics similar to bioavailable stream/riverine DOC would be helpful in determining the contribution of DOC in transport to ecosystem metabolism.

Stable and radioactive C isotopes are useful tracers for elucidating flow paths and transformations of dissolved and particulate organic C in lentic and lotic ecosystems (e.g., Bott et al. 1977, Dahm 1981, Hall 1995, Hall and Meyer 1998, Cole et al. 2002). Complex mixtures of ^{14}C-labeled compounds from leaf leachates have been used to examine stream DOC dynamics in

[1] Present address: Marine Science Department, University of Hawaii at Hilo, 200 West Kawili Street, Hilo, Hawaii 96720-4091 USA. E-mail: wiegner@hawaii.edu
[2] E-mail addresses: lakaplan@stroudcenter.org
[3] newbold@stroudcenter.org
[4] ostrom@pilot.msu.edu

laboratory mesocosms (Bott et al. 1977, Dahm 1981, 1984); however, radioisotopes generally cannot be released into the environment. To date, ^{13}C-labeled bicarbonate ($H^{13}CO_3^-$), an inorganic substrate for aquatic photosynthesis, and acetate ($^{13}C\text{-}CH_3O_2$), a volatile fatty acid, have been used to examine organic C dynamics in whole-ecosystem tracer additions (Hall 1995, Hall and Meyer 1998, Cole et al. 2002). However, stream DOC uptake dynamics cannot be completely elucidated using either bicarbonate or acetate as tracers. Bicarbonate tracks autochthonous C in streams, but most stream DOC is terrestrial in origin (Kaplan and Newbold 1993, Meyer et al. 1998, Palmer et al. 2001). Acetate is a labile monomeric organic molecule, whereas stream DOC is made up of a mixture of molecules, mostly polymeric in nature, that vary in their biological availability (Thurman 1985, Kaplan and Newbold 2003).

Therefore, to examine the dynamics of stream organic matter in the laboratory and field, deciduous trees were labeled with $^{13}CO_2$ to create a stable isotope tracer more representative of stream DOC than either bicarbonate or labile monomers (Wiegner et al. 2005). Leaf leachate, like stream DOC, is a mixture of organic molecules with substantial polymeric character and numerous lability fractions (Cummins et al. 1972, McClaugherty 1983, Thurman 1985, Qualls et al. 1991, Hongve 1999). A fresh extract of tree tissues is not a perfect model for stream DOC because it has not been extensively aged in the soil like most DOC entering streams. Nevertheless, DOC leached from leaf litter has been used to examine DOC dynamics in streams because leaf litter DOC can account for 30% of the daily DOC export from small, forested streams on an annual basis and as much as 42% of DOC inputs in the autumn (McDowell and Fisher 1976, Meyer et al. 1998).

Biological uptake of DOC is an enzymatic process (as reviewed in Arnosti 2003), so an accurate assessment of uptake rates requires attention to natural concentrations in the system under investigation. Many studies have examined leaf leachate uptake rates in stream systems (e.g., Cummins et al. 1972, Wetzel and Manny 1974, Lock and Hynes 1976, Dahm 1981), but most of the measurements in these studies were not accurate assessments of in situ DOC uptake because they were determined under highly elevated, and possibly saturating, DOC concentrations rather than at tracer levels, which are ideal for characterizing uptake dynamics of an element (Mulholland et al. 1990, Hart et al. 1992, Mulholland et al. 2002). In our study, ^{13}C-labeled tree-tissue leachate was used as a DOC tracer to examine DOC cycling within streambed sediments. Contributions of DOC in transport to stream ecosystem metabolism were estimated in mesocosms with streambed sediments from measurements of ^{13}C-DOC uptake, ^{12}C-DOC concentrations, and diel changes in dissolved O_2.

Methods

Study site

Water and sediments for the ^{13}C-DOC uptake experiment were collected from the east branch of White Clay Creek (WCC), a 3rd-order stream with intact riparian woodlands. The stream is located in the Piedmont Physiographic Province of southeastern Pennsylvania, USA (lat 39°53′N, long 75°47′W). WCC drains 725 ha of agricultural (52% equine/bovine pasture, 22% tilled/hayed) and wooded land (23%), and the 3rd-order reach is ~2400 m long (Newbold et al. 1997). The dominant tree species are beech (*Fagus grandifolia*), red and black oak (*Quercus rubra* and *Q. velutina*), and tulip poplar (*Liriodendron tulipifera*). The soils in the watershed are typic hypludults, except in the riparian zones, where aquic fragiudults predominate. Mean annual stream flow, stream water temperature, and local precipitation are 115 L/s, 10.6°C, and 105 cm, respectively (Newbold et al. 1997). The stream gradient is 0.008 m/m (Newbold et al. 1997). Streambed sediments are made up of clay-, silt-, and sand-sized particles in pools and runs, with gneiss- and schist-derived gravel and cobble in riffles (Kaplan et al. 1980). The stream has an estimated wetted area of 24,000 m^2 at base flow (Newbold et al. 1997).

Synthesis of a ^{13}C-labeled stream DOC tracer

Synthesis of a ^{13}C-labeled stream DOC tracer began in June 2001, when thirty-two 1-y-old tulip poplar seedlings were grown with $^{13}CO_2$ at the National Phytotron located at Duke University, Durham, North Carolina, USA (Wiegner et al. 2005). Tulip poplar trees were selected for this work because they are one of the most

TABLE 1. Mean (±1 SD) physical and environmental conditions in recirculating mesocosms, the artificial stream, and White Clay Creek (WCC) during ^{13}C-DOC uptake experiment. PAR = photosynthetically active radiation.

Variable	Mesocosm	Artificial stream	WCC
Velocity (m/s)	0.06	0.09 (±0.01)	0.16 (±0.1)
Depth (m)	0.83[a]	0.05 (±0.01)	0.06 (±0.03)
Temperature (°C)	22.0 (±0.5)	20.3 (±2.1)	20.3 (±1.6)
Light intensity (μmol photons m^{-2} s^{-1} PAR)	288 (±0.3)	62.7 (±0.8)	212 (±327)

[a] Effective depth of the mesocosm calculated as (volume of water in the mesocosm − volume of sediment tray)/(surface area of sediment tray). Effective depth of the mesocosms was used in calculations of mass transfer coefficients. See text for details. Actual depth of water directly above the sediment trays was 0.04 m

abundant trees in the WCC watershed, and they are ideal for stable isotope labeling because they grow rapidly. The ^{13}C-labeled tulip poplar trees were harvested, dried to a constant mass at 60°C, and ground in a Wiley Mill through a 250-μm-mesh sieve. Approximately 1 g of ground tree tissue (60.9% leaves, 24.6 % stems, 14.5% roots, based on tissue mass) was added to 1 L of filtered (0.2-μm polyethersulfone membrane; Gelman Supor®-200, East Hills, New York) deionized water (DIW). The mixture of all tree-tissue types (leaf, stem, and root) was used to generate a leachate representative of organic matter inputs from trees to streams. The water and plant material were stirred gently with a Teflon-coated stir bar in a 1-L glass container in the dark at 4°C for 24 h. After 24 h, the water and plant material were centrifuged at 17,931 × g for 0.5 h. The supernatant was filtered through a DIW-rinsed GF/F (Whatman, Clifton, New Jersey) filter and Tyndallized in 2 cycles (70°C water bath for 0.5 h, cycles separated by 24 h at room temperature) to ensure biological stability. The leachate was stored at 4°C in the dark for ~4 mo until the experiment began. The DOC concentration and δ^{13}C value of the leachate were 10.8 mmol C/L and 6095, respectively. All glassware and GF/F filters used in our study were combusted at 500°C for 6 h.

Sediment collection

Sandy sediments were collected from WCC during July 2002 and placed in 4 galvanized steel trays (19 cm [l] × 9 cm [w] × 3.75 cm [h]) with detachable bottoms perforated by 0.32-cm-diameter holes that allowed water exchange. The trays of streambed sediments were placed in an artificial stream located in a greenhouse to protect them from disturbance during storms. The artificial stream was fed with WCC water, and the water velocity and depth in the artificial stream were similar to the sampling site (Table 1). Three layers of black nylon screen were placed over the sediment trays to reduce algal growth during an 18-d incubation period.

^{13}C-DOC uptake experiment

Three of the 4 sediment trays were transferred to individual 15-L recirculating Plexiglas® mesocosms (Rapid Creek Research, Boise, Idaho) with Venturi flume inserts. The 4th sediment tray remained in the artificial stream and served as a reference for sediment characteristics before the ^{13}C-DOC uptake experiment. The Venturi flume improved control of current velocity over the sediments. The sediment trays were placed into the wells of the Venturi flumes with their top surfaces contiguous with the front ramps of the flumes, and the chambers were closed and filled with WCC water that had been filtered through a 3-stage glass-fiber cartridge filter system (Balston, Cleveland, Ohio) consisting of 75-, 25-, and 0.3-μm filters in series (Kaplan 1994). The depth of the water directly above the sediments was 0.04 m, a water depth similar to WCC (Table 1); the effective depth of the water above the sediments was 0.83 m ([mesocosm volume − sediment tray volume]/sediment tray area). Air bubbles were dislodged from the mesocosms, and water was recirculated through the system. The water velocity was controlled with a Tarpon Bay model pump speed controller (Rapid Creek Research) set to 0.06 m/s, a velocity similar to that measured in WCC prior to the experiment (Table 1). A water jacket filled with WCC water was used to con-

trol water temperature in the mesocosms. Photosynthetically active radiation (PAR) was supplied by 400-W halogen bulbs (coated MetalArc; OSRAM Sylvania, Danvers, Massachusetts) suspended above each mesocosm. The lights were placed on a timer with 14/10 h light/dark cycle, and the mesocosms were covered with black plastic at night to prevent room light from entering them.

Sondes with dissolved O_2 and temperature/conductivity probes (YSI Model 600 XL, Yellow Springs, Inc., Yellow Springs, Ohio) were inserted into the recirculation line of each mesocosm. O_2 and temperature were measured every 10 min and stored on a data logger (Covington Controller, Rapid Creek Research). Photosynthesis and respiration were measured for 1.5 h on day 1 of the experiment in the light and dark, respectively.

Eight mL of the ^{13}C-DOC tracer were injected into the mesocosm water, and uptake by the stream sediments was quantified with time series DOC (total DOC = ^{12}C + ^{13}C) and ^{13}C-DOC concentration measurements. The water volume in the mesocosms was maintained throughout the experiment by replacing the volume removed (320 mL) during sampling with an equal volume of filtered stream water (0.3-μm, glass fiber; Balston). Sampling times were based on previous measurements for glucose and arabinose uptake in WCC (Kaplan and Newbold 2003) and were selected to capture uptake lengths of 3 potential DOC lability classes, 2 similar to glucose and arabinose and 1 more refractory. Water samples were filtered (GF/F, Whatman) and DOC samples were analyzed immediately. Samples for isotope analysis were stored frozen in 250-mL plastic containers until analysis. In addition, initial and final water samples (40 mL) were formalin-fixed for epifluorescence microscopic counts (EMC) of suspended bacteria.

At the end of the experiment, the sediment trays from the mesocosms and artificial stream were sampled for bacterial abundance, organic matter content, chlorophyll *a* (chl *a*), and particle-size distribution. The upper 3 mm of the sediments were removed with an Exacto knife, placed in an aluminum weigh boat, homogenized, and subsampled by wet mass: 1 g for EMC, 5 to 6 g for organic matter content, 6 to 7 g for chl *a*, and the balance for particle-size analysis.

Analytical methods

Stream water chemistry.—DOC was measured by Pt-catalyzed persulfate oxidation using either an OI 700 or an OI 1010 (O. I. Corporation, College Station, Texas) C analyzer (Kaplan 1992). Preparation of DOC for isotope analysis followed the method of Gandhi et al. (2004). Samples (100–200 mL) were concentrated to 1 to 2 mL via rotary evaporation, and 300 μL of the concentrate were dried in a silver capsule and analyzed for C isotopes using an elemental analyzer (EA3000, Eurovector, Milan, Italy) interfaced to a PRISM (GV Instruments, Manchester, UK) stable isotope mass spectrometer. Stable C isotope ratios were expressed as:

$$\delta^{13}C = [(R_{SAMPLE}/R_{PDB}) - 1] \times 1000 \qquad [1]$$

where R is ^{13}C/^{12}C. The standard was V-PDB, and the reproducibility of these measurements at natural abundance levels was ≤0.2‰ and <27‰ at values >95‰ (Gandhi et al. 2004, Wiegner et al. 2005).

Bacterial abundance.—Bacterial abundance in sediment and water samples was measured from EMC after staining with propidium iodide (PI) (Sigma, St. Louis, Missouri; Bott and Kaplan 1993) according to a method modified from Battin et al. (2001). Formalin-preserved EMC samples were incubated in 5 mL of filtered (0.2-μm, Acrodisc®, HT Tuffryn® membrane; Pall Gelman Laboratory, East Hills, New York) 0.2-mol/L tetrasodium pyrophosphate for ≥0.5 h, and were subsequently sonicated (1.5 min, 50–70 W output) to detach the bacterial cells from the sediment (Velji and Albright 1985). The samples were vortexed, and 1 mL was transferred to a sterile Falcon tube with 1 mL of the tetrasodium pyrophosphate. The samples were incubated for 0.5 h, and subsequently were sonicated (50–70 W output). Following sonication, 2 mL of 60% glycerol were added and the samples were vortexed and centrifuged for 3 min at 853 × g to reduce background fluorescence from mineral particles. For sediment samples, 1 mL of the glycerol/sample suspension was transferred to a sterile Falcon tube and diluted 1:10 with 9 mL of 2.5% 0.2-μm-filtered formaldehyde. Water samples were not diluted. Samples (300–500 μL of diluted sediment suspensions or 500 μL–3 mL of undiluted stream water) were stained with 5 drops of PI (0.2 mg/L) and filtered onto a black 0.2-μm polycarbonate filter

(Poretics, Osmonics, Inc., Minnetonka, Minnesota). Bacterial cells were counted in 20 fields on a Zeiss Universal microscope equipped with epifluorescence illumination. Three filters were counted for each sediment or water sample.

Sediment organic matter and chl a.—Sediment organic matter content was determined as ash-free dry mass (AFDM). Sediments were placed in precombusted Al weigh boats, dried to a constant weight at 105°C, and ashed at 500°C for 6 h. Sediment chl *a* samples were centrifuged at 17,077 × g for 10 min and decanted, and pellets were frozen prior to extraction. Chl *a* was extracted with 15 mL of analytical-grade acetone at 0°C in the dark for 24 h. Following extraction, the sediments were vortexed, centrifuged at 17,077 × g for 10 min, and the absorbance of the supernatant was measured at 750 and 655 nm on a Perkin–Elmer Lambda 3B UV/VIS spectrophotometer. Two drops of 1 N HCl were added to the supernatant, and absorbance was measured again at 750 and 655 nm to correct for pheophytins (Lorenzen 1967).

Sediment particle size distribution.—Sediments were dried at 105°C to a constant mass and wet-sieved through a series of 4 sieves (53-μm, 106-μm, 1-mm, 4-mm mesh sizes). Particles that passed through the 53-μm sieve were further separated into 15- and 0.5-μm fractions using 15-μm-mesh Nitex netting and GF/F filters under vacuum, respectively.

Calculations

^{13}C-DOC uptake.—^{13}C enrichment (fractional abundance, F) in all DOC samples (stream water, mesocosm water, ^{13}C-leachate) was calculated using measured δ^{13}C-DOC values as:

$$F = R_{SAMPLE}/(R_{SAMPLE} + 1) = {}^{13}\mathrm{C}/({}^{12}\mathrm{C} + {}^{13}\mathrm{C}) \quad [2]$$

These data were then used in a mixing model to provide estimates of the fraction of C from the tree-tissue leachate in the bulk DOC pool (f_L) during the uptake experiment (Wiegner et al. 2005) as:

$$f_L = [(F_M - F_S)/(F_L - F_S)] \quad [3]$$

where F_M is the measured fractional abundance of ^{13}C-DOC in the mesocosms, F_S is the measured fractional abundance of ^{13}C-DOC in WCC water prior to the ^{13}C-leachate addition, and F_L is the measured fractional abundance of ^{13}C-DOC in the tree-tissue leachate. The ^{13}C-DOC concentration of the ^{13}C-leachate in the mesocosms ($^{13}C_L$) was calculated as:

$$^{13}C_L = f_L C_M F_L \quad [4]$$

where C_M is the DOC concentration measured in the mesocosm. C_M was calculated for each sampling time during the uptake experiment from measured δ^{13}C-DOC and DOC values. ^{13}C-DOC concentrations of the ^{13}C-leachate in the mesocosms were corrected for stream water dilution during the experiment.

DOC in stream water is not uniformly labile and the molecules making up this pool most likely represent a nearly continuous array of labilities. The temporal loss-rate curve for stream DOC was approximated from the sum of a few 1st-order loss rates for different DOC lability classes. Based on previous work with monomers and algal leachates in WCC (L.A. Kaplan and co-workers, unpublished data; J.D. Newbold and co-workers, unpublished data), our expectation was to resolve 2 to 3 DOC lability classes, ranging from readily labile (rapidly taken up) to refractory (undetectable uptake), in the ^{13}C-DOC tracer. An attempt was made to resolve 3 significant uptake rate coefficients for 3 individual DOC lability classes from the temporal uptake rate curve by nonlinear least squares analysis (SAS, version 8.1, SAS Institute, Cary, North Carolina). However, only 2 significant uptake rate coefficients (k_1, k_2) for the ^{13}C-DOC tracer were resolved. The equation used to calculate these coefficients was:

$$^{13}C_L = C_1 e^{-k_1 t} + C_2 e^{-k_2 t} \quad [5]$$

where C_1 and C_2 are the initial ^{13}C-DOC concentrations in the 2 DOC lability classes at the beginning of the experiment, and t is the elapsed time of the experiment. Uptake mass transfer coefficients (V_{f1}, V_{f2}) for these components were calculated from the equation:

$$V_f = k/h \quad [6]$$

where h is the effective water depth in the mesocosms (Stream Solute Workshop 1990). The uptake mass transfer coefficient is often thought of as the average vertical velocity at which a solute migrates through the sediment–water interface (Stream Solute Workshop 1990).

Metabolism.—Rates for net primary productivity (NPP) were calculated from increases in the dissolved O_2 concentration in the light (as de-

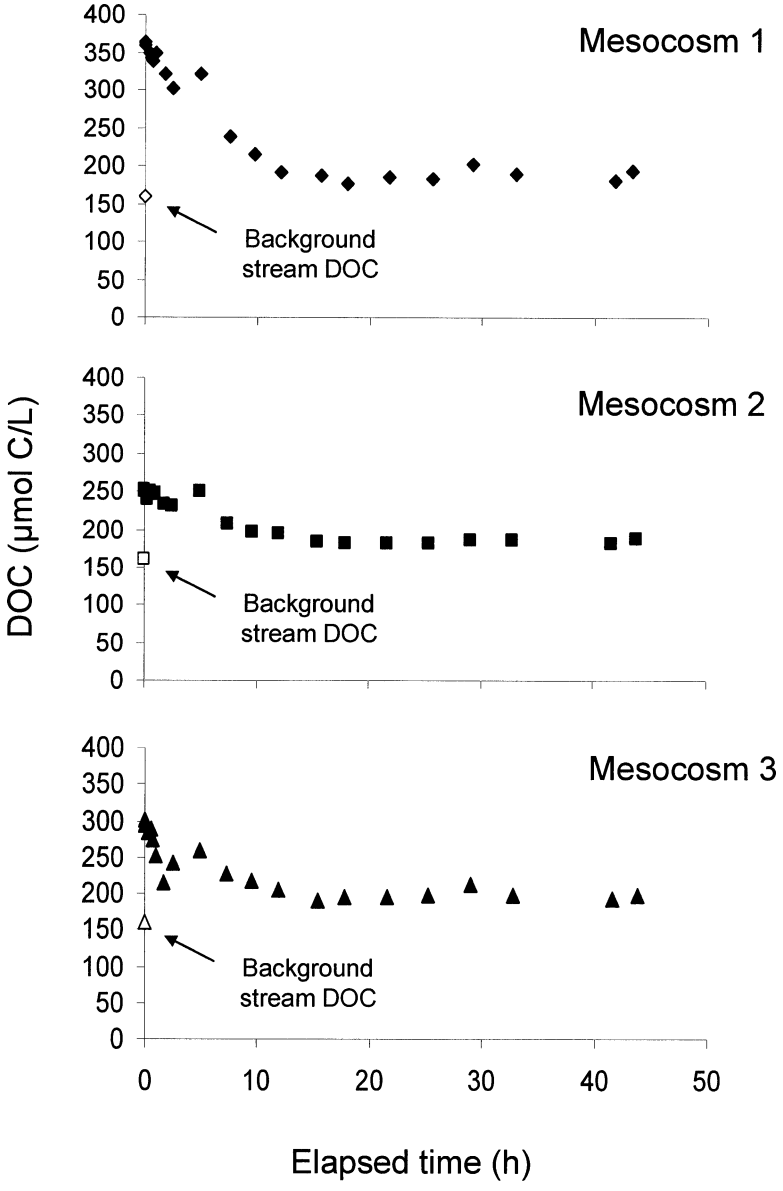

FIG. 1. Changes in dissolved organic C (DOC) concentration in the recirculating mesocosms during the ^{13}C-DOC uptake experiment. Background DOC concentration in the stream is shown for reference on each panel.

scribed in the section above). Respiration (RESP) rates were calculated from decreases in the dissolved O_2 concentration in the dark and are reported as positive values. Gross primary productivity (GPP) rates were estimated from the sum of the hourly rates for NPP and RESP (GPP = NPP + RESP). Net ecosystem metabolism (NEM) was calculated over a 24-h period as the difference between GPP and RESP (NEM = $GPP_{DAY} - RESP_{24\ h}$), assuming that the respiration rate was constant over a diel cycle (i.e., $RESP_{DAY} = RESP_{NIGHT}$). GPP, RESP, and NEM were converted to units of C assuming a photosynthetic and respiratory quotient of 1.35 and

TABLE 2. Mean (±1 SD) characteristics of sediments used in ^{13}C-dissolved organic C (DOC) uptake experiment in comparison to typical White Clay Creek (WCC) sediments. Chl *a* = chlorophyll *a*, DM = dry mass, RESP = respiration, GPP = gross primary productivity, NEM = net ecosystem metabolism. ND = measurements not made.

				Bacterial cell abundance	
Mesocosm	Median grain size (μm)	% Organic content[a]	Chl *a* (mg chl *a*/m^2)	Sediment (10^9 cells/g DM)	Water column (10^6 cells/mL)
Control	80.2	2.08 (±0.07)	226.52	1.1 (±0.6)	0.2 (±0.0)
1	81.3	2.22 (±0.49)	224.66	1.2 (±0.5)	1.4 (±0.2)
2	85.1	1.61 (±0.16)	227.08	1.1 (±0.3)	1.6 (±0.1)
3	77.1	2.29 (±0.16)	296.13	1.3 (±0.2)	1.4 (±0.1)
Mean	**80.9 (±3.3)**	**2.05 (±0.37)**	**243.60 (±35.04)**	**1.1 (±0.4)**	**1.5 (±0.2)[b]**
WCC	580 (±200)[c]	1.56 (±0.55)[c]	32.46 (±2.76)[d]	4.7 (±3.2)[e]	0.4[f]

[a] Determined as ash-free dry mass (AFDM)
[b] Mean of 3 experimental mesocosms
[c] Taken from Bott and Kaplan 1985
[d] T. L. Bott, Stroud Water Research Center, personal communication; mean (±1 SD) from wooded reach in WCC during summers 1997, 2000, and 2001
[e] Taken from Kaplan et al. 1992 (intact core)
[f] Taken from Battin et al. 2003

0.85, respectively (Hutchinson 1957, Vollenweider 1974).

Results

DOC was released initially from all 3 sediment trays when they were placed in the mesocosms (Fig. 1). This DOC increased the DOC concentration of the stream water by 91% (±34) (mean ±1 SD). The sediments used in the experiment were consistently heterotrophic (RESP > GPP; Table 2). The absolute rates of GPP and RESP in the mesocosms were 3× higher than rates measured in a wooded reach of WCC, but the degree of heterotrophy was comparable to whole-stream estimates of NEM (Table 2). Sediment tray chl *a* concentrations were 8× higher and bacterial abundances were 4× lower than values for streambed sediments sampled directly from WCC.

The ^{13}C-labeled DOC tracer addition increased the stream DOC by 3% and was used rapidly in all 3 mesocosms. Overall, 80% (±5) of the ^{13}C-DOC added to the mesocosms was consumed (Fig. 2). Regressions fit to the temporal ^{13}C-DOC uptake curves were significant ($p \leq 0.001$) and revealed 2 distinct lability classes in the leachate (Table 3). The 2 DOC pools were categorized as readily and intermediately labile based on their uptake coefficients. The readily and intermediately labile components made up 88% (±0.6) and 12% (±0.6), respectively, of the biodegradable DOC (BDOC) (expressed as % of the initial ^{13}C-DOC taken up in the experiment). Significant uptake coefficients ($p < 0.05$) were estimated for the readily labile component of the leachate in all 3 mesocosms (Table 3). The estimated uptake rate coefficient for one mesocosm was 2× higher than the values for the other 2 mesocosms, but the confidence intervals for all 3 mesocosms overlapped (Table 3). This difference among the mesocosms in the uptake coefficients for the readily labile component of the leachate also affected the estimated uptake mass transfer coefficients (Table 3). In contrast, only one of the estimated uptake coefficients measured for the intermediately labile ^{13}C-DOC pool was significant (mesocosm 2, $p < 0.05$), but the estimated uptake rate coefficients were similar (Table 3). Estimated uptake mass transfer coefficients were ~16 to 30× faster for the readily labile component of the ^{13}C-DOC (V_{f1}) than for the intermediately labile component (V_{f2}).

Discussion

Stream sediment characteristics

The pulse of DOC (^{12}C and ^{13}C) released from mesocosm sediments was a disturbance artifact associated with the transfer of sediments from

TABLE 2. Extended.

RESP (mmol C m^{-2} d^{-1})	GPP (mmol C m^{-2} d^{-1})	NEM (mmol C m^{-2} d^{-1})
ND	ND	ND
260.20	169.55	−90.66
177.72	128.32	−49.40
185.77	127.45	−58.32
207.90 (±45.48)	**141.77 (±24.06)**	**−66.13 (±21.71)**
82.86 (±36.39)[d]	42.82 (±37.27)[d]	−40.04 (±52.11)[d]

the artificial stream to the mesocosms (Fig. 1). This DOC release increased the mesocosm water column DOC by 91% (±34) and overwhelmed the DOC pulse from the ^{13}C-DOC tracer addition. Nevertheless, the release was symptomatic of DOC dynamics operating within benthic sediments where DOC is produced and consumed simultaneously. These results demonstrated that measuring in situ stream DOC uptake dynamics is complicated by processes that continually produce, transform, and consume DOC molecules in transport and that bulk DOC measurements alone cannot distinguish among different C pools. As a result, both bulk DOC and isotope measurements were needed to determine ^{13}C-DOC uptake dynamics. We were able to measure ^{13}C-DOC uptake by stream sediments directly with the use of a DOC isotope tracer and mixing model. ^{13}C-DOC uptake was most likely dominated by biological processes; the sediments used in our study were in equilibrium with mesocosm-water DOC and the ^{13}C-DOC was added at tracer levels. In addition, previous work with WCC sediments has shown negligible abiotic uptake of DOC from stream water and other terrestrial sources (Kaplan and Bott 1985).

The 18-d incubation period in the artificial stream prior to the ^{13}C-uptake experiment altered the characteristics of the streambed sediments used in our experiment (GPP, RESP, chl *a* concentrations, bacterial abundance) relative to sediments sampled directly from the stream (Table 2). However, NEM was similar between the sediments from the mesocosms and those from WCC (Table 2). NEM is a mea-

TABLE 3. ^{13}C-dissolved organic C (DOC) uptake parameters from mesocosm experiment. Estimates (95% confidence intervals) for initial concentrations of the readily (C_1) and intermediately (C_2) labile ^{13}C-DOC pools are shown with their uptake rate coefficients (k_1, k_2) and uptake mass transfer coefficients (V_{f1}, V_{f2}). See text for details.

	Mesocosm		
Variable	1	2	3
Readily labile			
C_1 (nmol ^{13}C/L)	609 (366–853)	371 (339–403)	363 (217–510)
k_1 (/h)	0.19 (0.047–0.33)	0.36 (0.28–0.44)	0.17 (0.058–0.29)
V_{f1} (μm/s)	43	83	40
Intermediately labile			
C_2 (nmol ^{13}C/L)	190 (−73–455)	206 (176–237)	176 (23–330)
k_2 (/h)	0.011 (−0.030–0.052)	0.011 (0.0067–0.017)	0.011 (−0.014–0.035)
V_{f2} (μm/s)	2.5	2.7	2.5

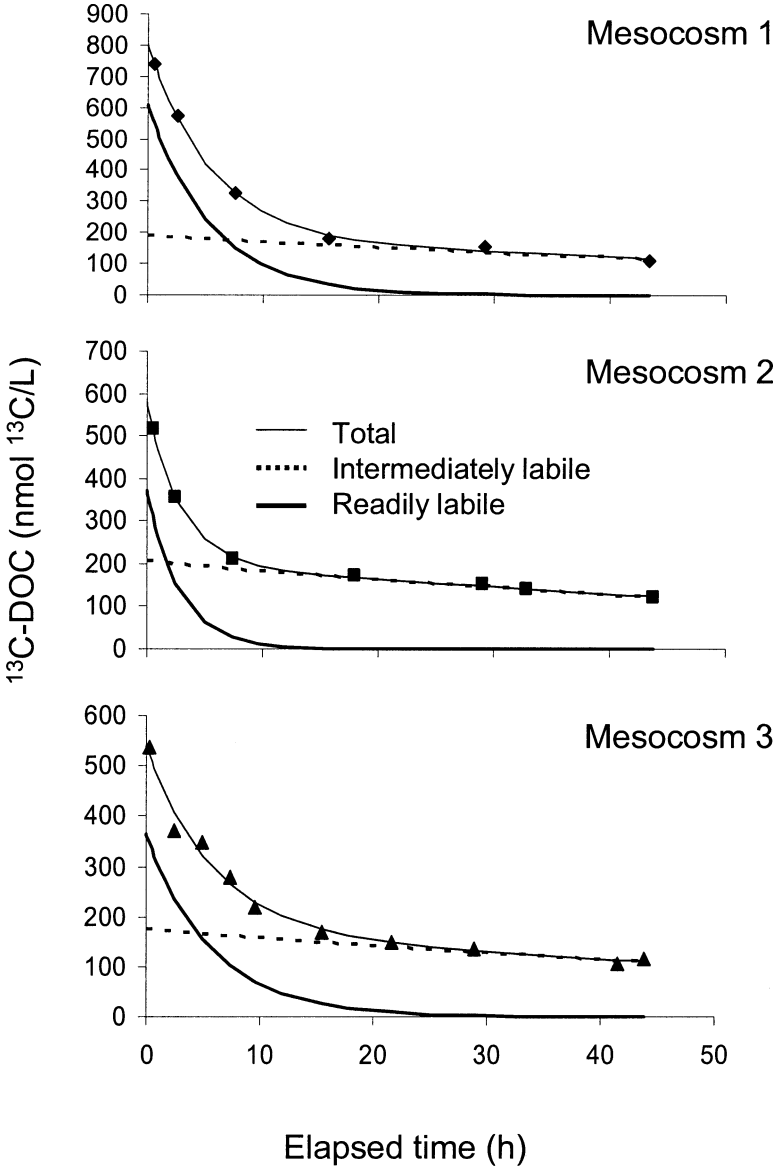

FIG. 2. Dilution-corrected changes in ^{13}C-dissolved organic C (DOC) concentration during the ^{13}C-DOC uptake experiment. Symbols indicate measured values of ^{13}C-DOC at each sampling time. Calculated uptake curves for total, readily labile, and intermediately labile ^{13}C-DOC are shown. See text for details of calculation of uptake curves.

sure of the balance between GPP and RESP, which controls whether an ecosystem is autotrophic or heterotrophic. The trophic status of a stream and its sediments, in large part, affects the importance of DOC in transport as an energy source. The sediments from the mesocosms and WCC were equally heterotrophic (Table 2), suggesting that they both had a similar demand for allochthonous C. Hence, the metabolism measurements from our mesocosms were used to estimate DOC dynamics in WCC.

Comparison of DOC uptake dynamics with inorganic N and P

As nutrients are transported downstream, they cycle between dissolved and particulate forms from the water column to the streambed in a spiral-like path (Webster and Patten 1979). The tightness of a nutrient spiral reflects the relationship between the supply of the nutrient and the metabolic activity in the stream (Minshall et al. 1983). Insights into which nutrients limit stream and riverine metabolic activity can be gained by comparing spiraling dynamics for different nutrients. Nutrient uptake lengths are influenced by scaling effects of water depth and velocity, as well as by nutrient concentrations and the stream biota. Thus, the uptake mass transfer coefficient (V_f), a concentration-normalized uptake velocity ($V_f = U/C$, where U = solute uptake rate/unit area of stream bottom and C = in situ solute concentration), was used to compare nutrient uptake dynamics among streams and to scale the mesocosm results to the whole stream (Stream Solute Workshop 1990). Unlike nutrient uptake lengths, the uptake mass transfer coefficient describes the transfer of nutrients across the water–sediment interface independently of the scale (water depth and velocity) of the stream (Stream Solute Workshop 1990).

Uptake of allochthonous DOM has been examined in many natural and artificial stream systems, including WCC (Table 4). The median V_{f1} for the readily labile fraction of the ^{13}C-DOC in our study was 11 to 25× larger than median values of V_f previously measured for leaf leachates and other allochthonous DOC sources to WCC, and 54× greater than values of V_f measured for DOC in WCC base flow and storm flow (Table 4). The values of V_f measured for the readily labile component of the ^{13}C-DOC in our study and the leachates in other studies should have been similar because they were all composed of relatively fresh DOC (not aged in soils) derived from leaf litter whose bioavailability is generally high (i.e., Lock and Hynes 1975). Most, if not all, of the values of V_f for these leachates probably were underestimates of their in situ values because they were measured under highly elevated DOC concentrations that probably saturated their uptake kinetics ($V_f = U_{max}/(K_s + C)$, where U_{max} is the maximum uptake rate at saturating solute concentrations and K_s is the half-saturation constant; Mulholland et al. 2002). In contrast, the V_{f1} for the ^{13}C-DOC in our study was similar to values of V_f measured for both glucose and acetate, whose uptake was measured at near-tracer levels (Table 5). These results demonstrate that the readily labile component of the ^{13}C-DOC in our study is representative of easily used organic molecules. This finding is further supported by the fact that the ^{13}C-DOC contained some known, readily labile molecules like glucose and fructose (Wiegner et al. 2005). The intermediately labile component of the ^{13}C-DOC in our study had a V_f similar to those measured for leaf leachates and other allochthonous DOC sources to WCC. However, as mentioned above, this comparison may not be appropriate because the values of V_f for these DOC sources probably were underestimated. A more accurate comparison would be that the V_{f2} for the ^{13}C-DOC in our study was similar to values of V_f measured for DOC in WCC base flow and storm flow (Table 4). This comparison suggests that this component of the ^{13}C-DOC may be more representative of the bulk DOC in WCC than the readily labile component.

Few studies have compared stream uptake dynamics of C, N, and P, and even fewer have measured them simultaneously (Munn and Meyer 1990). We compared our results to median V_f values for labile DOC, NH_3, NO_3, and PO_4 from isotope-tracer addition studies and nutrient enrichment studies across lentic systems. The V_{f1} of the ^{13}C-DOC in our study was similar to values of V_f measured for NH_3, glucose, and acetate, 3× larger than the values of V_f measured for NO_3, but only ½ that measured for PO_4 (Tables 4, 5), suggesting that easily used DOC is not as strongly retained as PO_4 in streams (Tables 4, 5). In comparison, the V_{f2} for the ^{13}C-DOC in our study was 1 to 2 orders of magnitude smaller than any values of V_f measured for NH_3, NO_3, and PO_4 (Tables 4, 5), suggesting that intermediately labile DOC travels further downstream than inorganic N or P before it is taken up by the stream sediments.

Contribution of DOC in transport to stream ecosystem metabolism

Benthic bacteria dominate community respiration in many stream and river ecosystems (Fisher and Likens 1973, Edwards et al. 1990). Thus, the fuel driving benthic bacterial respi-

TABLE 4. Comparison of dissolved organic C (DOC) uptake dynamics in experiments conducted in the field, artificial streams, and mesocosms. Uptake rates (U) and uptake mass transfer coefficients (V_f) for different DOC sources are shown. Median values for U and V_f were calculated from all reported measurements from cited literature; n = the number of observations used for median calculation. WCC = White Clay Creek, NA = data not available, – = information not applicable.

DOC source	System	Experiment type	Experiment duration (h)
Leaf leachate			
Alnus rubra	Oak Creek, Oregon	Mesocosm	48
A. rubra	Devil's Club, Oregon	Mesocosm	8
A. rubra	Mack Creek, Oregon	Mesocosm	8
A. rubra	Lookout Creek, Oregon	Mesocosm	8
Populus tremloides	Hard water	Mesocosm	9
P. tremuloides	Soft water	Mesocosm	9
Betula alleghaniensis	Bear Brook, New Hampshire	Field	5
Tsuga occidentalis	Hard water	Mesocosm	9
T. occidentalis	Soft water	Mesocosm	9
Acer saccharum	Hard water	Mesocosm	9
A. saccharum	Soft water	Mesocosm	9
A. saccharum	Speed River, Canada	Mesocosm	9
A. saccharum	Bear Brook, New Hampshire	Field	5
A. circinatum	Grasshopper Creek, Oregon	Mesocosm	4
A. circinatum	Quartz Creek, Oregon	Mesocosm	4
A. circinatum	Mack Creek, Oregon	Mesocosm	4
Pinus resinosa	Hard water	Mesocosm	9
P. resinosa	Soft water	Mesocosm	9
Picea rubens	Bear Brook, New Hampshire	Field	5
Carya glabra/*A. saccharum*	Augusta Creek, Michigan	Artificial stream	48
Forest litter leachate[a]	West Creek, Pennsylvania	Mesocosm	2.5
Forest litter leachate[a]	White Clay Creek, Pennsylvania	Mesocosm	2.5
Forest litter leachate[b]	Saw Mill Springs, Pennsylvania	Mesocosm	2.5
Leaf leachate/sucrose	Big Hurricane Branch/Hugh White Creek, North Carolina	Field	1–2
Median (n = 32)			
Liriodendron tulipifera (readily labile)	White Clay Creek, Pennsylvania	Mesocosm	48
Median (n = 3)			
L. tulipifera (intermediately labile)	White Clay Creek, Pennsylvania	Mesocosm	48
Median (n = 3)			
Other allochthonous DOC sources to WCC			
Impatiens capensis	White Clay Creek, Pennsylvania	Mesocosm	NA
I. capensis	West Creek, Pennsylvania	Mesocosm	2.5
Median (n = 13)			
Lindera benzoin	White Clay Creek, Pennsylvania	Mesocosm	NA
Median (n = 2)			
Bovine manure	White Clay Creek, Pennsylvania	Mesocosm/ Field	2.5–5
Bovine manure	West Creek, Pennsylvania	Mesocosm	2.5
Bovine manure	Saw Mill Springs, Pennsylvania	Mesocosm	2.5
Median (n = 8)			
WCC DOC			
Base flow	White Clay Creek, Pennsylvania	Field	NA
Storm flow	White Clay Creek, Pennsylvania	Mesocosm	NA
Median (n = 6)			

[a] Includes data from whole leachate and low- and high-molecular-weight fractions
[b] Includes data from low- and high-molecular-weight fractions

TABLE 4. Extended.

Stream DOC (μmol C/L)	Experiment DOC (μmol C/L)	DOC increase from leachate addition (%)	U (mmol C m^{-2} h^{-1})	V_f (μm/s)	Reference
100	917	817	1.2	0.4	Dahm 1981
183	600	228	2.0	1.3	Dahm 1984
183	600	228	0.9	0.6	Dahm 1984
208	625	200	0.9	0.6	Dahm 1984
1233	4528	268	10.0	0.8	Lock and Hynes 1975
482	3728	673	9.2	0.8	Lock and Hynes 1975
125	542	334	10.4	6.9	McDowell 1985
790	1737	120	2.3	0.7	Lock and Hynes 1975
842	1475	75	1.9	0.8	Lock and Hynes 1975
790	3172	302	6.1	0.7	Lock and Hynes 1975
842	3392	303	4.2	0.5	Lock and Hynes 1975
1375	3075–3617	123–163	9.3–9.8	1.2–1.6	Lock and Hynes 1976
125	433–592	246–374	6.1–9.4	3.9–6.7	McDowell 1985
250	750	200	3.5	2.0	Dahm 1984
183	683	273	3.3	1.9	Dahm 1984
350	850	143	0.7	0.4	Dahm 1984
790	1696	115	3.3	1.0	Lock and Hynes 1975
842	1584	88	0.8	0.3	Lock and Hynes 1975
125	610	366	10.8	6.6	McDowell 1985
250	3217	1187	18.3	1.7	Cummins et al. 1972, Wetzel and Manny 1974
NA	375	NA	1.7–4.2	1.2–3.1	Kaplan and Bott 1985
NA	375	NA	2.5–6.0	1.9–4.4	Kaplan and Bott 1985
NA	375	NA	5.4–8.3	4.0–6.2	Kaplan and Bott 1985
83	–	–	20	66.7	Meyer et al. 1988
			4.9	**1.7**	
160	164	2.5	2.9–5.9	40–83	This study
			3.1	**43**	
160	164	2.5	0.18–0.20	2.5–2.7	This study
			0.18	**2.5**	
117–767	375–1045	81–562	1.6–20.2	0.8–10.6	Kaplan and Bott 1983, 1985, Kurserk et al. 1984
NA	375	NA	7.5	5.6	Kaplan and Bott 1985
			7.5	**3.8**	
NA	402	NA	6.0–12.1	4.1–8.4	Kaplan and Bott 1983
			9.0	**6.2**	
283–677	641–1034	60–127	0.8–19.8	0.6–8.2	Kurserk et al. 1984, Kaplan and Bott 1985
NA	375	NA	5.7–9.2	4.2–6.8	Kaplan and Bott 1985
NA	375	NA	1.7	1.2	Kaplan and Bott 1985
			5.0	**4.3**	
157–667	–	–	0.5–1.4	0.6–0.9	Kaplan and Bott 1983, Kurserk et al. 1984
403–767	–	–	0.3–5.2	0.2–1.9	Kaplan and Bott 1983
			1.1	**0.8**	

TABLE 5. Comparison of C, N, and P uptake dynamics across streams. Nutrient uptake lengths (S_w) and uptake mass transfer coefficients (V_f) for different streams are shown. Median values for S_w and V_f were calculated from all reported measurements from cited literature; n = number of observations used in each median calculation. DOC = dissolved organic C.

System	Discharge (L/s)	S_w (m)	V_f (μm/s)
DOC			
Hugh White Creek, North Carolina	4.1[a]	87[a]	146[b]
W2 H. J. Andrews Forest, Oregon	1[a]	357[a]	5.23[b]
Coweeta Hydrologic Laboratory, North Carolina[c]	0.81–2.13	8–12	16–47[b]
White Clay Creek, Pennsylvania	41–44	346–352	26–46
White Clay Creek, Pennsylvania	41–44	847–1405	9–12
Median (n = 11)		**347**	**26**
NH_3			
La Solana, Spain	20.7	121	76[d]
Riera Major, Spain	57.8	137	216[d]
Hugh White Creek, North Carolina	5.5	30[e]	58[f]
Walker Branch, Tennessee	7.6–9.6	20–43	69–150[f]
Eagle Creek, Michigan	191–208	766–1349	31–50[f]
Kuparuk River (6 streams), Alaska	21–18,300	40–5360	61–1990[d]
Hubbard Brook (13 streams), New Hampshire[g]	0.4–86.6	5–271	14–180
Kings Creek, Kansas	2–48	24–261	4–394
Quebrada Bisley, Puerto Rico	11.3–18.4	16–26	146–180
Grand Teton National Park (11 streams), Wyoming	4–231	77–925[h]	18–210
Ball Creek, North Carolina	42.7	28	687
Sycamore Creek, Arizona	66	47	255
Gallina Creek, New Mexico	5.7	21	154
Mack Creek, Oregon	87.4	54	200
East Fork Little Miami River, Ohio	849	474	122
Median (n = 82)		**63**	**60**
NO_3			
Hugh White Creek, North Carolina	4.1[a]	689[a]	11[b]
W2 H. J. Andrews Forest, Oregon	1[a]	42[a]	99[b]
La Solana, Spain	20.7	161	57[d]
Riera Major, Spain	57.8	49	600[d]
Cliff Creek, Idaho	83.3	1839	23
Pioneer Creek, Idaho	88	549	82
Walker Branch, Tennessee	8.5–9.6	101–511	5–31[f]
Hubbard Brook (8 streams), New Hampshire[g]	0.6–86.6	16–9585[h]	0.3–27
Kings Creek, Kansas	4–55	168–402	7–124
Quebrada Bisley, Puerto Rico	11.3–18.4	1192–>3000	0.4–3
Grand Teton National Park (8 streams), Wyoming	12–231	108–2412[h]	6–150
Median (n = 37)		**407**	**14**
PO_4			
Walker Branch, Tennessee	2.6–9.4	22–455	11–70[d]
Hugh White Creek, North Carolina	4.1[a]	85[a]	311[b]
W2 H. J. Andrews Forest, Oregon	1[a]	697[a]	5[b]
La Solana, Spain	20.7	89	104[d]
Riera Major, Spain	57.8	177	167[d]
Cliff Creek, Idaho	83.3	370	113
Pioneer Creek, Idaho	88	370	121
Hubbard Brook (10 streams), New Hampshire	0.4–86.6	2–85	32–193
Median (n = 42)		**34**	**97**

TABLE 5. Extended.

Addition type	Reference
Sucrose enrichment	Munn and Meyer 1990
Sucrose enrichment	Munn and Meyer 1990
Acetate tracer	Hall and Meyer 1998
Glucose enrichment	L.A. Kaplan and co-workers, unpublished data
Arabinose enrichment	L.A. Kaplan and co-workers, unpublished data
Enrichment	Martí and Sabater 1996
Enrichment	Martí and Sabater 1996
Tracer	Hall et al. 1998
Tracer, enrichment	Mulholland et al. 2000a,b
Tracer	Hamilton et al. 2001
Tracer	Wollheim et al. 2001
Tracer, enrichment	Bernhardt and Likens 2002, Hall et al. 2002, Webster et al. 2003
Tracer, enrichment	Dodds et al. 2002
Tracer	Merriam et al. 2002
Enrichment	Hall and Tank 2003
Tracer	Webster et al. 2003
Tracer	Webster et al. 2003
Tracer	Webster et al. 2003
Tracer	Webster et al. 2003
Tracer	Webster et al. 2003
Enrichment	Munn and Meyer 1990
Enrichment	Munn and Meyer 1990
Enrichment	Martí and Sabater 1996
Enrichment	Martí and Sabater 1996
Enrichment	Davis and Minshall 1999
Enrichment	Davis and Minshall 1999
Tracer, enrichment	Mulholland et al. 2000a,b
Enrichment	Bernhardt and Likens 2002, Bernhardt et al. 2002
Enrichment	Dodds et al. 2002
Tracer	Merriam et al. 2002
Enrichment	Hall and Tank 2003
Tracer, enrichment	Newbold et al. 1983, Mulholland et al. 1985, 1990
Enrichment	Munn and Meyer 1990
Enrichment	Munn and Meyer 1990
Enrichment	Martí and Sabater 1996
Enrichment	Martí and Sabater 1996
Enrichment	Davis and Minshall 1999
Enrichment	Davis and Minshall 1999
Enrichment	Hall et al. 2002

TABLE 5. Footnotes.

[a] Mean across cobble, gravel, debris dams, and rock outcrop habitats
[b] V_f calculated from uptake rate (U) and solute concentration (C) as $V_f = U/C$
[c] Includes data from reference and leaf-litter-excluded streams (streams C53 and C55)
[d] V_f calculated from stream velocity (v), depth (h), and S_w as $V_f = vh/S_w$
[e] Mean S_w for epilithon, wood, leaves, and moss from 23-d field data
[f] V_f calculated from stream discharge (Q), width (w), and solute S_w as $V_f = (Q/w)/S_w$
[g] Includes data from streams that received DOC additions
[h] S_w calculated from stream velocity (v), depth (h), and V_f as $S_w = vh/V_f$

ration drives ecosystem metabolism. In the mesocosms, benthic bacteria most likely dominated community respiration because 99% of the bacteria were benthic, and because algal respiration, estimated as 25% of GPP (Geider and Osborne 1989), would have accounted for only 17% of the total system respiration (Table 2). Several lines of evidence suggest that DOC in transport is an important energy source for benthic bacteria. First, epilithic bacterial metabolism in forested streams is not tightly coupled to epilithic algal production (Findlay et al. 1993a, Rosenfeld and Hudson 1997), even though algal exudates are labile (Kaplan and Bott 1982, 1989). Second, simultaneous decreases in DOC, dissolved O_2, and bacterial production and increases in dissolved inorganic C concentration in stream and river sediments have been noted in field and mesocosm studies (Findlay et al. 1993b, Fischer et al. 2002b, Sobczak and Findlay 2002). Below, results from the ^{13}C-DOC mesocosm experiment are placed into an ecosystem context by assessing the importance of DOC in transport to stream metabolism under 2 scenarios where either DOC or GPP contribute maximally to heterotrophic metabolism.

In the 1st scenario, the maximum contribution of DOC in transport to benthic bacterial C demand was estimated by assuming that all DOC removed from the water column was metabolized. For this assessment, bacterial C demand and the mass flux of DOC from the water column to the sediments were calculated, and their rates were compared. Bacterial respiration was assumed to dominate heterotrophic respiration, and bacterial respiration was calculated as community respiration minus algal respiration (algal respiration = 25% of GPP; Geider and Osborne 1989). Algal respiration accounted for 17% of community respiration in our mesocosm sediments. This value is just slightly higher than typical rates reported for WCC sediments (13%; Table 2). Bacterial respiration was converted to benthic bacterial C demand by assuming 30% bacterial growth efficiency on riverine DOC (del Giorgio and Cole 1998). The DOC in the ^{13}C-DOC tracer was assumed to be similar in quality to the BDOC in WCC (25% of the DOC in WCC is BDOC; Volk et al. 1997). Specifically, we assumed that ½ of the BDOC concentration (DOC = 160 μmol C/L, 40 μmol BDOC/L; ½ BDOC = 20 μmol C/L) had an uptake mass transfer coefficient similar to V_{f1} and the other ½ had an uptake mass transfer coefficient similar to the V_{f2} (Table 3). This assumption was based on the fact that ½ of BDOC in WCC is made up of readily labile molecules (carbohydrates [30%], amino acids [4%], unidentified molecules [13%]), and the other ½ is made up of intermediately labile humic substances (Volk et al. 1997). Chemical analyses of the ^{13}C-DOC supported this assumption; known readily labile (i.e., glucose and fructose) and intermediately labile (i.e., humic substances and polysaccharides) molecules found in stream water have been identified in the tracer (Wiegner et al. 2005). The BDOC concentrations were multiplied by V_{f1} and V_{f2}, respectively, and the 2 resulting fluxes were summed to estimate the delivery of DOC in transport to the streambed. DOC in transport supported 54% (±31) of the bacterial C demand and 51% (±28) of community respiration in the mesocosm sediment trays under this scenario.

In the 2nd scenario, the maximum contribution of GPP to benthic bacterial C demand was estimated by assuming that primary production and bacterial production were coupled and that benthic bacteria metabolized all newly produced autotrophic C (Table 2). For this assessment, bacterial C demand and net stream algal production were calculated and their rates compared. DOC in transport was assumed to support any remaining bacterial C demand not sus-

tained by algal production. Net stream primary production (NPP′) was calculated by subtracting algal respiration from GPP (see preceding paragraph). Based on the estimate for bacterial C demand calculated in the preceding paragraph, 67% (±5) of the bacterial C demand in our mesocosms was supported by NPP′ (NPP′/bacterial C demand × 100) and the remaining 33% (±5) was supported by nonalgal C ([bacterial C demand − NPP′]/[bacterial C demand] × 100). Assuming that this allochthonous C was DOC in transport, 82% (±48) of the DOC transported from the water column to the sediments would have been metabolized ([bacterial C demand − NPP′]/[DOC flux] × 100) under this scenario.

The ultimate source of C sustaining heterotrophic bacterial metabolism is DOC even though significant relationships between benthic respiration, benthic bacterial abundance, and production have been observed with particulate organic C (POC) concentrations in sediments (e.g., Bott and Kaplan 1985, Edwards et al. 1990, Hedin 1990, Sobczak et al. 1998, Brunke and Fischer 1999). DOC may be taken up directly from water passing through the sediments or may come indirectly from benthic POC sources such as algal exudates, buried POC (from degradation), and DOC previously adsorbed to either the sediment biofilm or particles (Fiebig and Lock 1991, Fiebig 1992, Findlay and Sobczak 1996, Battin et al. 1999). Stream and river sediments biologically and chemically immobilize a significant fraction of DOC passing through them (Fiebig and Lock 1991, Battin et al. 1999, Brugger et al. 2001, Fischer et al. 2002a). Previous studies have found that DOC in transport can support 11 to 55% of the benthic bacterial metabolism in streams and rivers (Bott et al. 1984, Findlay et al. 1993b, Fischer et al. 2002a, Sobczak and Findlay 2002). In our mesocosms, DOC in transport supported 33 to 54% of the bacterial C demand, depending on the importance of NPP′ as a C source. These results are consistent with previous estimates for WCC where 55% of benthic bacterial biomass (Bott et al. 1984) and 39% of hyporheic respiration (end-member mixing model, Battin et al. 2003) were supported by DOC in transport.

Fate of DOC in streams

To determine the fate of DOC in transport in WCC, uptake lengths (S_{w1}, S_{w2}) for readily and intermediately labile DOC, similar in quality to the ^{13}C-DOC tracer, were calculated using the equation:

$$S_w = vh/V_f \quad [7]$$

where v and h were the velocity and depth of the stream at the time stream sediments were collected for the mesocosm experiment (Table 1) and V_f was the uptake mass transfer coefficient for the readily labile (V_{f1}) and intermediately labile (V_{f2}) components of the ^{13}C-DOC, as measured in the mesocosms (Table 3; Stream Solute Workshop 1990). The uptake length of a dissolved nutrient is the average distance it travels in the water column before being taken up by the sediments (Newbold et al. 1981). Assuming that values of V_f measured in the mesocosms were representative of DOC uptake in the stream, the readily and intermediately labile DOC would travel 175 and 3692 m, respectively, in WCC before being taken up by the sediments. These distances represent ~7% and >150%, respectively, of the length of the 3rd-order reach. Thus, readily labile DOC should be an important energy source at the reach scale, whereas intermediately labile DOC should provide an energy link between upstream and downstream reaches, as originally proposed in the River Continuum Concept (Vannote et al. 1980). Further research is needed to quantify the pathways by which DOC from different lability classes and sources (autochthonous vs allochthonous) is transferred to higher trophic levels in aquatic ecosystems. Links between microbial and grazing food webs can be established by combining isotope techniques with whole-system measurements, and these links can be used to address the question of whether bacteria are a source or sink for C in aquatic ecosystems (Ducklow et al. 1986, Cole et al. 2002).

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