2014

Modeling priming effects on microbial consumption of dissolved organic carbon in rivers

Michelle A. Baker, *Utah State University*

AGU PUBLICATIONS

JGR

Journal of Geophysical Research: Biogeosciences

RESEARCH ARTICLE
10.1002/2013JG002599

Key Points:
- We estimated priming of soil and river DOC decay by algal leachates and glucose
- Modeled priming of soil and river DOC decay ranged from -130 to +370%
- Our results demonstrate that the priming effect can augment DOC decay in rivers

Correspondence to:
E. R. Hotchkiss,
ehotchkiss@gmail.com

Citation:
Hotchkiss, E. R., R. O. Hall Jr., M. A. Baker, E. J. Rosi-Marshall, and J. L. Tank (2014), Modeling priming effects on microbial consumption of dissolved organic carbon in rivers, *J. Geophys. Res. Biogeosci.*, *119*, 982–995, doi:10.1002/2013JG002599.

Received 20 DEC 2013
Accepted 25 APR 2014
Accepted article online 1 MAY 2014
Published online 29 MAY 2014

Modeling priming effects on microbial consumption of dissolved organic carbon in rivers

E. R. Hotchkiss[1,2], R. O. Hall Jr.[1], M. A. Baker[3], E. J. Rosi-Marshall[4], and J. L. Tank[5]

[1]Program in Ecology and Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA, [2]Now at Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden, [3]Department of Biology and the Ecology Center, Utah State University, Logan, Utah, USA, [4]Cary Institute of Ecosystem Studies, Millbrook, New York, USA, [5]Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana, USA

Abstract Rivers receive and process large quantities of terrestrial dissolved organic carbon (DOC). Biologically available (unstable) DOC leached from primary producers may stimulate (i.e., prime) the consumption of more stable terrestrially derived DOC by heterotrophic microbes. We measured microbial DOC consumption (i.e., decay rates) from contrasting C sources in 10 rivers in the western and Midwestern United States using short-term bioassays of river water, soil and algal leachates, glucose, and commercial humate. We added inorganic nutrients (ammonium and phosphorus) to a subset of bioassays. We also amended a subset of river, soil, and commercial humate bioassays with glucose or algal leachates to test the hypothesis that unstable DOC primes consumption of more stable DOC. We used prior measurements of source-specific DOC bioavailability, linked with a Bayesian process model, to estimate means and posterior probability distributions for source-specific DOC decay rates in multisource bioassays. Modeled priming effects ranged from a −130 to +370% change in more stable DOC decay when incubated with unstable DOC. Glucose increased modeled river DOC decay by an average of 87% among all rivers. Glucose and algal leachates increased soil leachate and commercial humate decay by an average of 25% above background rates. Inorganic nutrient additions did not have consistent effects on DOC decay, likely because most of the study rivers had high ambient background nutrients. Our results demonstrate that the priming effect can augment DOC decay in rivers. In addition, Bayesian models can be used to estimate mechanisms driving aquatic ecosystem processes that are difficult to measure directly.

1. Introduction

Freshwater ecosystems receive, process, and transport organic and inorganic carbon (C) inputs from terrestrial ecosystems. At least half of the C inputs to freshwater ecosystems are outgassed to the atmosphere or stored in sediments before reaching the oceans [*Cole et al*., 2007; *Aufdenkampe et al*., 2011; *Raymond et al*., 2013]. Fluxes of C in freshwater can be higher than C fluxes in terrestrial ecosystems on an areal basis and can account for measurable portions of terrestrial ecosystem production [*Cole et al*., 2007]. Breakdown of terrestrial organic C (OC) in streams, lakes, and rivers is considerably faster than in soil [*Battin et al*., 2008; *Bianchi*, 2011], and a greater proportion of terrestrially derived macromolecules may break down in freshwater ecosystems than in terrestrial soils [*Ward et al*., 2013; *Guenet et al*., 2014]. Furthermore, terrestrial OC inputs can support animal secondary production in freshwater food webs [*Hall et al*., 2001; *Carpenter et al*., 2005; *Cole et al*., 2011] and fuel the heterotrophic state of most freshwater ecosystems [*Fisher and Likens*, 1973; *Cole and Caraco*, 2001; *Duarte and Prairie*, 2005]. Because of the large role of terrestrial subsidies in freshwater C fluxes and cycling, understanding drivers of terrestrial OC turnover will aid in quantifying the role of freshwater ecosystems in continental and global-scale C budgets [*Cole et al*., 2007].

Dissolved organic carbon (DOC) is the principal downstream OC flux in rivers [*Schlesinger and Melack*, 1981; *Alvarez-Cobelas et al*., 2011] and it serves as a primary source of OC for heterotrophic microbes [*Battin et al*., 2008]. Accordingly, quantifying how DOC is processed and transported is a crucial step in understanding how freshwater ecosystems process all OC. The structure and availability of DOC has been linked to its source: internal (i.e., autochthonous) production of DOC via photosynthesis is generally more biologically available and less stable than terrestrially derived (i.e., allochthonous) DOC [*Moran and Zepp*, 1997; *Farjalla et al*., 2009; *Guillemette et al*., 2013]. While autochthonous OC production likely sustains a large portion of stream DOC processing and subsequent CO_2 efflux, transformation and processing of allochthonous DOC also supports

whole-ecosystem C cycling [*Cole and Caraco*, 2001; *Carpenter et al*., 2005; *Fellman et al*., 2009]. Additionally, terrestrial OC pools can be sources of low molecular weight DOC that is highly bioavailable if transported to freshwater ecosystems before being consumed by soil microbes [*Berggren et al*., 2010]. DOC processing by microbes, linked with the abiotic breakdown of complex organic matter by UV radiation, may increase the availability of allochthonous DOC to other stream biota [*Wetzel et al*., 1995; *De Lange et al*., 2003; *Amado et al*., 2006] and contribute to the high turnover rates of terrestrial OC in freshwater ecosystems [*Battin et al*., 2008].

Inputs of bioavailable OC can increase the rate at which microbes consume more stable OC, a process termed the "priming effect" [*Bingeman et al*., 1952; *Guenet et al*., 2010; *Kuzyakov*, 2010]. Potential mechanisms of priming include (1) enzymes produced to degrade unstable OC can also breakdown more stable OC, (2) microbial density increases in response to unstable OC sources, resulting in increased breakdown of more stable OC, or (3) cometabolism between microbes that specialize on more and less stable OC [*Fontaine et al*., 2003, 2004a; *Guenet et al*., 2010]. UV radiation may also prime terrestrial OC for more rapid microbial decay [*Brandt et al*., 2010; *Guenet et al*., 2010]. Research examining controls on OC storage and mineralization in soils has identified multiple drivers of priming effects, including primary production, substrate quality and quantity, microbial biomass and composition, background nutrient concentrations, environmental conditions, and structure and availability of OC [*Kuzyakov et al*., 2000; *Guenet et al*., 2010; *Kuzyakov*, 2010].

Although the priming effect has rarely been studied in freshwater ecosystems, priming may increase microbial uptake of more stable DOC in streams and rivers by 10–500% [*Guenet et al*., 2010, 2014; *Bianchi*, 2011]. Algal and macrophyte exudates may provide bioavailable DOC to prime the consumption of terrestrial OC in freshwater ecosystems [*Farjalla et al*., 2009; *Danger et al*., 2013; *Kuehn et al*., 2014], and heterotrophic bacteria can readily consume exudates from primary producers [*Cole et al*., 1982; *Baines and Pace*, 1991; *Farjalla et al*., 2009]. While some microbes preferentially consume unstable DOC and reduce consumption of more stable OC (a "negative priming effect"), the presence of unstable DOC may prime microbes to consume additional stable OC (a "positive priming effect") [*Thouin et al*., 2009; *Lutz et al*., 2012; *Guenet et al*., 2014]. We hypothesize that priming of terrestrial DOC consumption through the use of autochthonous DOC by microbes may be partially responsible for high turnover of terrestrial OC in freshwater ecosystems.

We used short-term biological assays and 2-pool decay models assessed via Bayesian methods to identify rates and drivers of DOC consumption by microbes in rivers, and to test the following predictions: (1) Microbes consume glucose and algal leachates at faster rates than river DOC, soil leachates, and commercial humate. (2) Glucose and algal leachate additions will prime additional microbial consumption of more stable river DOC, soil leachates, and commercial humate in multisource DOC bioassays. (3) We can identify priming effects of unstable DOC additions by combining traditional bioassays with a multicompartment Bayesian process model.

We quantified microbial DOC decay rates of different C sources in bioassays with river DOC, algal leachates, soil leachates, glucose, or commercial humate using site-specific microbes from 10 rivers in the western and Midwestern United States. We used a Bayesian multicompartment model to estimate changes in more and less stable DOC pool decay rates in bioassays with combined DOC sources. To test for a priming effect of unstable DOC, we compared background rates of river, soil, and commercial humate decay with decay rates in assays supplemented with less stable glucose or algal leachates.

2. Methods

2.1. Dissolved Organic Carbon Concentrations and Decay Rates

We collected samples during base flow from five rivers in the Midwestern United States and five rivers in the western United States during summer 2011 and 2012, respectively. Rivers were mostly turbid and had moderate to high nutrient concentrations (Table 1). We selected these rivers as part of a larger study measuring nutrient and C cycling across a range of suspended sediment loads and ambient nutrient concentrations. To measure background DOC concentrations, we filtered water using preashed glass fiber filters (Whatman GF/F), acidified triplicate samples to pH 2 with HCl, and stored samples in acid washed and ashed borosilicate amber vials. Samples were kept cool until analysis on a Shimadzu Total Organic Carbon Analyzer (TOC-5000A; measurement precision of ± 0.05 mg C L^{-1}).

Table 1. Physical and Water Chemistry Characteristics of Study Rivers[a]

River	River ID	Discharge ($m^3 s^{-1}$)	Velocity ($m s^{-1}$)	Depth (m)	Turbidity (Nephelometric Turbidity Unit (NTU))	NH_4^+ ($\mu g N L^{-1}$)	NO_3^- ($\mu g N L^{-1}$)	SRP ($\mu g P L^{-1}$)	River DOC ($mg C L^{-1}$)	Soil Leachates ($mg C L^{-1}$)	Algal Leachates ($mg C L^{-1}$)
St. Joseph River, IN	STJ	25.3	0.43	1.2	4.0	32	1100	11	2.83	5.27	6.72
Tippecanoe River, IN	TIP	18.1	0.59	0.6	16.6	15	1850	67	4.32	13.41	5.33
East Fork White River, IN	WRE	13.5	0.36	0.8	42.8	1	1650	60	1.53	5.89	2.47
Muskegon River, MI	MUS	34.7	0.49	1.1	23.0	14	330	9	4.90	12.68	6.46
Manistee River, MI	MAN	37.1	0.52	1.4	2.9	30	120	10	1.74	8.60	6.64
North Platte River, WY	NPL	83.3	0.98	1.0	19.2	5	20	20	5.27	9.48	NA (not applicable)
Bear River, UT	BEA	15.8	0.45	1.0	53.1	12	49	18	4.08	7.26	NA
Green River, Ouray, UT	GRO	37.4	0.53	0.6	16.1	2	7	3	3.09	5.82	NA
Green River, Gray Canyon, UT	GRG	40.5	0.39	1.3	606.9	14	19	22	3.48	13.35	NA
Colorado River, UT	COL	63.7	0.57	1.3	115.8	1	697	12	2.98	4.36	NA

[a]These data were collected within 3 days of starting bioassay incubations for each river.

To obtain a site-specific proxy for terrestrial DOC, we leached riparian soil at each river in closed buckets of unfiltered river water for 24 h before filtering soil leachate for bioassays. At the Midwestern rivers, we collected dominant river primary producers by physically removing macrophytes or algal filaments from the river bottom, rinsing in the river to remove sediment, and placing directly in a bucket of river water to capture leachates. We leached collections of the dominant river algae or macrophyte assemblage (hereafter, algae) for at least 2 h in buckets of unfiltered river water exposed to sunlight to maximize algal production and exudation of autochthonous DOC for bioassays. Finally, we added glucose (corn sugar, Northern Brewer Homebrew Supply) to ultrapure water (Milli-Q Plus, EMD Millipore) with a target final concentration of 2 mg C L^{-1} to estimate microbial consumption of a standard form of highly bioavailable DOC. We chose a 2 mg C L^{-1} target spike in bioassay DOC to avoid increasing total C by more than 2 times background concentrations and to prevent depleting the glucose pool before the end of incubations. We added 5 mL filtered river water to glucose bioassays to avoid mineral nutrient limitation of glucose consumption in Milli-Q water. River DOC contributed to only 1.9–6.2% of total starting DOC in glucose bioassays with 5 mL river water additions. At the western rivers, we also added a commercially available humate extract of approximately 23% humic acid (Nature's Solution Ancient Humate, Nature Technologies International LLC) to a subset of Milli-Q and river water bioassays with a target concentration of 2 mg C L^{-1} to estimate microbial consumption of a more standardized form of humic terrestrial DOC.

We estimated rates of microbial DOC consumption using short-term biological assays [*Servais et al.*, 1989]. We filtered river water, soil and algal leachates, and commercial humate through preashed glass fiber filters (Whatman GF/F) into acid washed and ashed 250 mL amber borosilicate bottles. We added a 1% (by volume) inoculum of river microbes filtered through 2 μm Whatman filter capsules to remove large particulates. To estimate the role of inorganic nitrogen (N) and phosphorus (P) in limiting DOC decay rates, we amended a subset of river, soil, algal, and humate bioassays with target concentrations of 350 μg N-NH_4^+ L^{-1} (as NH_4Cl) and 50 μg P-PO_4 L^{-1} (as K_2HPO_4). We incubated bioassay bottles in coolers (~20°C) for 3–5 days (four replicate bottles per treatment) and refiltered and acidified water to measure final DOC concentrations. DOC bioassays were coupled with two types of controls: (1) incubations of filtered water without a microbial inoculum to ensure that microbes added to bioassays were solely responsible for DOC uptake and (2) incubations with

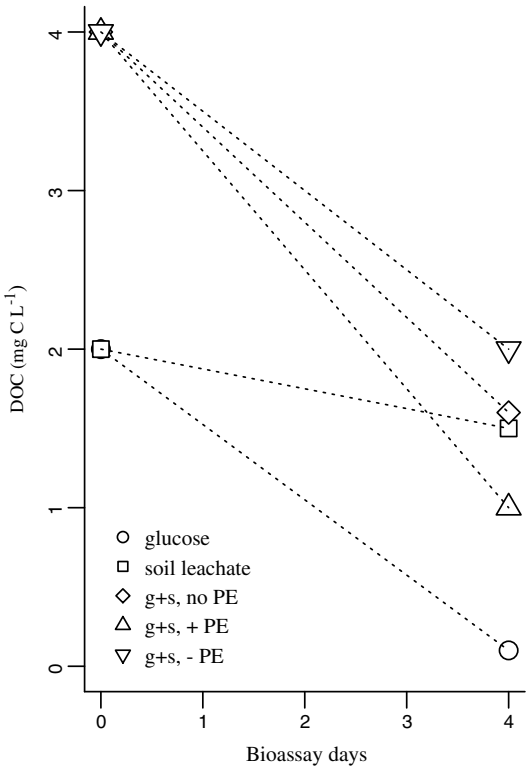

Figure 1. A graphical example of source-specific and multi-source DOC decay bioassay measurements. The hypothetical decay of "glucose" and "soil leachate" assumes each single DOC source bioassay started with 2 mg C L^{-1} and that glucose is much more bioavailable than soil leachate. When glucose and soil leachate are combined in a mixed DOC source bioassay ("g + s" trend lines), it is difficult to estimate negative (−), no, or positive (+) priming effects (PE) without knowing the proportion of glucose and soil leachate that was previously available to microbes. One exception would be if microbes consumed all of the glucose, and soil leachate decay rates were stimulated to produce final bioassay DOC concentrations below expected background rates of DOC decay. Lines are for ease of interpretation and do not represent a linear decay trajectory.

only Milli-Q water. We note that there were no measureable decreases in DOC concentrations in bioassays without microbes or increases in bioassays of Milli-Q water due to bottle or vial contamination. We used the difference in DOC concentrations before and after the incubations to calculate total DOC decay rates based on first-order uptake kinetics (k_{tot}; day^{-1}):

$$C_t = C_0 e^{-k_{tot} t} \quad (1)$$

C_0 and C_t represent DOC concentrations (mg C L^{-1}) at the start and end of t bioassay incubation days, respectively. We then used a Bayesian inverse model to estimate a posterior mean and probability distribution for k_{tot} (see parameter estimation below).

2.2. Two-Compartment DOC Decay Model and Bayesian Parameter Estimation

Traditional bioassay measurements are used to calculate a single first-order decay rate for DOC based on changes in total DOC concentration over time. In reality, that bulk rate reflects the decay of multiple DOC pools, each with its own decay rate. Because we wanted to estimate decay rates for unstable (e.g., glucose) and more stable (e.g., soil leachate) DOC pools when they were combined in a single bioassay (to examine the potential priming effect on soil leachate decay by glucose), we adapted equation (1) to solve for two unknown decay rates (Figure 1). This modification allowed us to compare changes in more and less stable DOC pools between (1) prior source-specific measurements of decay from unstable only and more stable only bioassays and (2) source-specific decay of both DOC pools when combined in a bioassay to test for priming.

We combined river DOC with glucose and soil leachates with glucose in bioassays at all 10 river sites to quantify microbial consumption and test for a priming effect of glucose on more stable river or soil DOC (Table 2). To test for a priming effect of site-specific autochthonous C on soil leachate decay, we combined algal and soil leachates at Midwestern sites (Table 2). At western sites, we combined commercial humate and glucose in DOC bioassays to test for a priming effect of glucose on commercial humate decay, allowing us to test site differences in microbial DOC consumption and priming of an identical terrestrial DOC source at all sites (Table 2). We excluded the potential for UV breakdown of terrestrial OC in rivers to play a role in our tests of priming by leaching soil in the dark and using dark bioassay bottles.

We expanded the first-order decay model (equation (1)) into a two-compartment first-order decay model to test for a priming effect in bioassays with DOC from multiple sources [after *Manzoni et al.*, 2012]:

$$C_{tot(t)} = p_1 C_{1(t0)} e^{-k_1 t} + p_2 C_{2(t0)} e^{-k_2 t} \quad (2)$$

where $C_{tot(t)}$ is the total concentration of combined DOC pools (C_1 and C_2) after t bioassay days, p_1 and p_2 are the proportions of the total DOC pool, and DOC decay rates (k_1 and k_2) differ by pool. Instead of holding k_1 constant to solve for a potential change in k_2, we used an inverse modeling approach, linked with

Table 2. Bioassay Treatments to Test for Priming Effects of River and Terrestrial DOC Consumption by River Microbes[a]

Less Stable DOC Source[b]	Site Specific?	More Stable DOC Source[c]	Site Specific?	Rivers	Combined More and Less Stable DOC Sources to Test:
Glucose	No	River	Yes	All ($n = 10$)	Priming of river DOC uptake with additions of glucose (with and without nutrient amendments).
Glucose	No	Soil	Yes	All ($n = 10$)	Priming of soil leachate uptake with additions of glucose (with and without nutrient amendments).
Algae	Yes	Soil	Yes	Midwest ($n = 5$)	Priming of soil leachate uptake with additions of algal leachate (with and without nutrient amendments).
Glucose	No	Commercial humate	No	West ($n = 5$)	Priming of humate uptake with additions of glucose (with and without nutrient amendments).

[a]All microbial additions to bioassays were site-specific.
[b]Priors for less stable DOC sources were inoculated bioassays with glucose in ultrapure water or algal leachates in river water.
[c]Priors for more stable DOC sources were inoculated bioassays with river DOC only, soil leachates in river water, or commercial humate in ultrapure water.

Bayesian parameter estimation, to simultaneously estimate posterior probability distributions for k_1 and k_2 that best predicted final bioassay DOC concentrations ($C_{tot(t)}$). For example, this expanded equation allowed us to estimate the pool-specific decay rates of glucose (k_1) and soil leachate (k_2) in bioassays with glucose-spiked soil leachate (Figure 1). Thus, a potential priming effect of glucose on soil leachate decay (k_2) can be estimated by comparing modeled k_2 to k_{tot} from bioassays with soil leachate only.

In using Bayesian parameter estimation, we included prior information about k_1 and k_2 from single-pool bioassays. We estimated posterior probability distributions for k_1 and k_2 using the Bayes rule: the joint posterior probability distribution of k_1 and k_2, given the DOC data, is proportional to the product of the DOC decay model likelihood and the prior probability distributions of unknown parameters [*Hilborn and Mangel*, 1997]. We simulated the posterior probability distributions for k_1 and k_2 using the *rjags* package and Markov chain Monte Carlo (MCMC) sampling from a proposed prior distribution [*R Core Team*, 2012; *Plummer*, 2013]. To estimate posterior probability distributions for k_1 and k_2, we used pool-specific starting DOC concentrations and prior information about pool-specific k rates measured in single DOC pool bioassays. Each model was run for 500,000 iterations using three different starting values within our prior distributions to ensure convergence on the same posterior parameter estimate. We did not thin MCMC chains [*Link and Eaton*, 2012]. We subtracted the first 1000 iterations of burn-in time based on visual assessments of MCMC chain behavior before calculating parameter posterior distribution means and credible intervals.

Table 3. Rates of Source-Specific DOC Decay and % River DOC Available[a]

River	k_{river} (day^{-1})	% Bioavailable River DOC	$k_{glucose}$ (day^{-1})	k_{soil} (day^{-1})	k_{algae} (day^{-1})	k_{humate} (day^{-1})
STJ	0.006 (0.007)	4.5 (2.5)	0.176 (0.079)	0.024 (0.004)	0.092 (0.005)	NA
TIP	0.002 (0.006)	0.0 (0.8)	0.445 (0.091)	0.024 (0.002)	0.038 (0.006)	NA
WRE	0.023 (0.016)	12.3 (1.4)	0.633 (0.074)	0.004 (0.004)	0.074 (0.013)	NA
MUS	0.007 (0.005)	3.2 (1.3)	0.117 (0.021)	0.001 (0.003)	0.075 (0.005)	NA
MAN	0.012 (0.013)	8.3 (2.1)	0.187 (0.064)	0.023 (0.003)	0.098 (0.005)	NA
NPL	0.028 (0.008)	11.6 (2.6)	0.401 (0.024)	0.017 (0.004)	NA	0.269 (0.044)
BEA	0.024 (0.010)	9.0 (2.3)	0.298 (0.026)	0.011 (0.004)	NA	0.214 (0.036)
GRO	0.018 (0.009)	6.6 (1.9)	0.181 (0.011)	0.058 (0.005)	NA	0.063 (0.015)
GRG	0.002 (0.013)	3.5 (2.8)	0.209 (0.051)	0.026 (0.003)	NA	0.228 (0.130)
COL	0.017 (0.010)	9.4 (0.9)	0.220 (0.008)	0.052 (0.007)	NA	0.081 (0.002)
Midwest	0.010 (0.010)	5.6 (4.9)	0.312 (0.066)	0.015 (0.003)	0.075 (0.007)	NA
West	0.018 (0.010)	8.0 (3.1)	0.262 (0.024)	0.033 (0.005)	NA	0.171 (0.046)
All	0.014 (0.010)	6.8 (4.1)	0.287 (0.045)	0.024 (0.004)	NA	NA

[a]Measured in short-term bioassays and calculated using Bayesian estimations. Standard deviations for each bioassay treatment ($n = 4$ per site) are noted in parentheses. These source-specific decay rates and standard deviations were used as prior probability distributions in the mixed DOC source models to estimate priming effects.

Table 4. Tests for Association Between Paired River Water Chemistry Variables and Bioassay Decay Rates[a]

Water Chemistry Variable	Bioassay DOC Sources	Correlation Coefficient	Bayes Factor[b]
DOC (dissolved organic carbon)	River	−0.19	0.27
	Soil	−0.30	0.33
	Algal	−0.56	0.55
	Commercial humate	0.76	1.10
	Glucose	−0.11	0.24
NO_3^- (nitrate)	River	−0.29	0.33
	Soil	−0.22	0.28
	Algal	−0.70	0.84
	Commercial humate	−0.52	0.50
	Glucose	0.61	1.37
NH_4^+ (ammonium)	River	−0.58	1.11
	Soil	−0.28	0.32
	Algal	0.53	0.51
	Commercial humate	0.69	0.81
	Glucose	−0.39	0.44
SRP (soluble reactive phosphorus)	River	−0.11	0.24
	Soil	−0.38	0.42
	Algal	−0.79	1.29
	Commercial humate	0.91	3.58[c]
	Glucose	0.86	35.38[d]
NTU (nephelometric turbidity units)	River	−0.37	0.41
	Soil	0.09	0.24
	Algal	−0.35	0.38
	Commercial humate	0.29	0.35
	Glucose	−0.15	0.25

[a]Pearson's product moment correlation tests and Bayes factors for correlation provided evidence for linear relationships.
[b]A Bayes factor of 3–10 or >10 provides substantial or strong evidence in support of a linear relationship.
[c]Substantial evidence.
[d]Strong evidence.

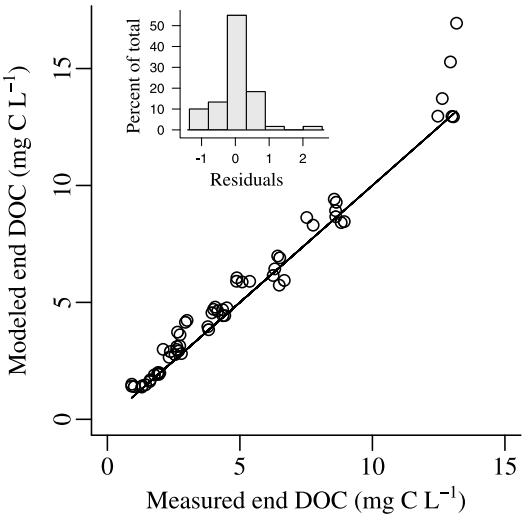

Figure 2. A comparison of measured versus modeled final bioassay DOC concentrations using posterior estimates of primed refractory DOC uptake (equation (2)) to confirm that modeled posterior DOC decay rates would produce realistic final bioassay DOC concentrations. Each point represents the mean DOC of a site-specific bioassay treatment; the solid line represents the 1:1 line. Points falling along the 1:1 show that the two-source DOC decay rate model did not overestimate or underestimate posterior means for k_{tot} (linear model $r^2 = 0.97$). Inset shows the frequency of residuals.

2.3. Statistical Analyses

We estimated mean priming effects among all sites by calculating the mean difference between prior and posterior stable DOC decay rates using Bayesian parameter estimation. As with a paired *t* test, our test for positive priming was supported if the mean priming effect ($k_{posterior} - k_{prior}$) was greater than 0. We simulated posterior probability distributions for mean priming effects using the Bayesian parameter estimation with the *rjags* package and MCMC sampling described above [*R Core Team*, 2012; *Plummer*, 2013].

We used a Bayesian *t* test alternative (Bayesian estimation supersedes the *t* test; *BEST* R package), to compare differences between means and credible intervals of source-specific DOC decay rates and regional DOC concentrations [*R Core Team*, 2012; *Meredith and Kruschke*, 2013]. If *BEST* 95% high density intervals (HDI) for the difference of means overlapped 0, we characterized the comparison of interest as one with no credible difference between treatments [*Kruschke*, 2013].

To identify environmental drivers of DOC decay and priming effects, we used Pearson's product

Table 5. Modeled Effect of Unstable DOC Additions on More Stable Dissolved Organic Carbon (DOC) Decay Rates[a]

Priming Treatment[b]	2.5%	50%	97.5%	*n* (# Rivers)
River DOC + glucose	0.0010	0.0047	0.0085	10
River DOC + glucose + NP	−0.0041	0.0042	0.0124	10
Soil leachate + glucose	−0.0003	0.0021	0.0044	10
Soil leachate + glucose + NP	0.0014	0.0027	0.0040	10
Soil leachate + algal leachate	−0.0036	−0.0001	0.0035	5
Soil leachate + algal leachate + NP	−0.0023	0.0012	0.0047	5
Commercial humate + glucose	−0.0307	0.0592	0.1444	5
Commercial humate + glucose + NP	−0.0252	0.0486	0.1197	5

[a]Mean effects above zero are evidence for a positive priming effect. Means (50% quantile) are the difference between prior and posterior more stable DOC decay rates among all river sites and bioassay replicates. Percentages are the Bayesian credible interval quantiles for each priming effect test.
[b]NP represents the ammonium and phosphorus amendments.

moment correlation tests to detect significant associations between river water chemistry and bioassay decay rates as well as between water chemistry and treatment priming effects [*R Core Team*, 2012]. We calculated Bayes factors for correlation, which identify the strength of evidence for linear relationships between two variables using Pearson correlation coefficients [*Wetzels and Wagenmakers*, 2012]. A Bayes factor of 1–3, 3–10, or >10 provides anecdotal, substantial, or strong evidence in support of a linear relationship [*Wetzels and Wagenmakers*, 2012]. A Bayes factor >3 is considered substantial evidence in support of a linear relationship, as the probability of a linear relationship is at least 3 times more likely than the null hypothesis of no relationship [*Wetzels and Wagenmakers*, 2012].

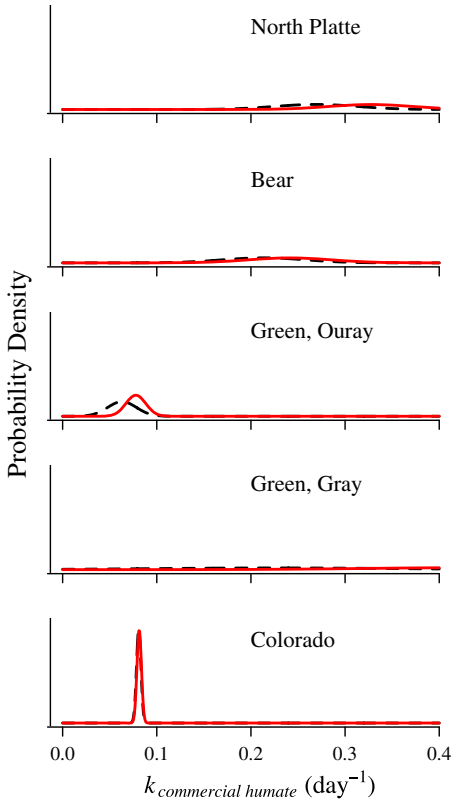

Figure 3. Prior (dashed line) and posterior (solid line) probability distributions for commercial humate decay rates with and without glucose. Prior commercial humate decay was estimated from commercial humate bioassays; posterior commercial humate decay was estimated from combined commercial humate + glucose DOC bioassays to model the potential priming of commercial humate by glucose (equation (2)).

3. Results

3.1. Biological Availability of DOC

River DOC concentrations varied among sites, but all site DOC concentrations were below 6 mg C L^{-1} at the time of sampling (Table 1). Mean DOC concentrations did not differ between Midwestern versus western rivers (95% HDI = −2.21,3.62). Soil leachate concentrations were variable, did not differ by region (95% HDI = −9.80,7.25), and ranged from 4.36 to 13.41 mg C L^{-1} (Table 1). Leached autochthonous DOC at the Midwestern sites increased DOC concentrations above background by at least 0.9 mg C L^{-1} and as much as 4.9 mg C L^{-1} (Table 1).

DOC decay rates varied by C source more than by river or region, despite the range in water chemistry and suspended sediment loads in the 10 rivers we sampled. Mean river DOC decay rates were 0.010 and 0.018 day^{-1} in the Midwestern and western rivers (Table 3), but there was no credible difference between regions (95% HDI = −0.03,0.01). There was no substantial evidence for correlations between river DOC decay rates and water chemistry variables (Table 4). River DOC decay rates were 20 times lower than glucose decay rates at all sites (95% HDI = −0.35,−0.18), which ranged from 0.117 to 0.633 day^{-1} (Table 3). Microbial glucose consumption was positively correlated with river soluble reactive phosphorus (SRP) concentrations (Table 4).

Table 6. Tests for Association Between Paired River Water Chemistry Variables and Modeled Priming Effect[a]

Water Chemistry Variable	Bioassay DOC Sources	Correlation Coefficient	Bayes Factor[b]
DOC (dissolved organic carbon)	River + glucose	0.26	0.30
	Soil + glucose	0.01	0.23
	Soil + algal	0.27	0.35
	Commercial humate + glucose	0.10	0.31
NO_3^- (nitrate)	River + glucose	−0.44	0.53
	Soil + glucose	−0.41	0.47
	Soil + algal	−0.16	0.32
	Commercial humate + glucose	−0.42	0.42
NH_4^+ (ammonium)	River + glucose	0.25	0.30
	Soil + glucose	−0.11	0.24
	Soil + algal	−0.06	0.31
	Commercial humate + glucose	0.74	1.00
SRP (soluble reactive phosphorus)	River + glucose	−0.44	0.53
	Soil + glucose	−0.51	0.74
	Soil + algal	−0.31	0.36
	Commercial humate + glucose	0.61	0.62
NTU (nephelometric turbidity units)	River + glucose	0.13	0.25
	Soil + glucose	0.00	0.23
	Soil + algal	0.13	0.32
	Commercial humate + glucose	0.92	4.11[c]

[a]The priming effects were calculated as the pooled difference between prior and posterior more stable DOC decay rates (Table 4). Pearson's product moment correlation tests and Bayes factors for correlation provided evidence for linear relationships.
[b]A Bayes factor of 3–10 provides substantial evidence in support of a linear relationship.
[c]Substantial evidence.

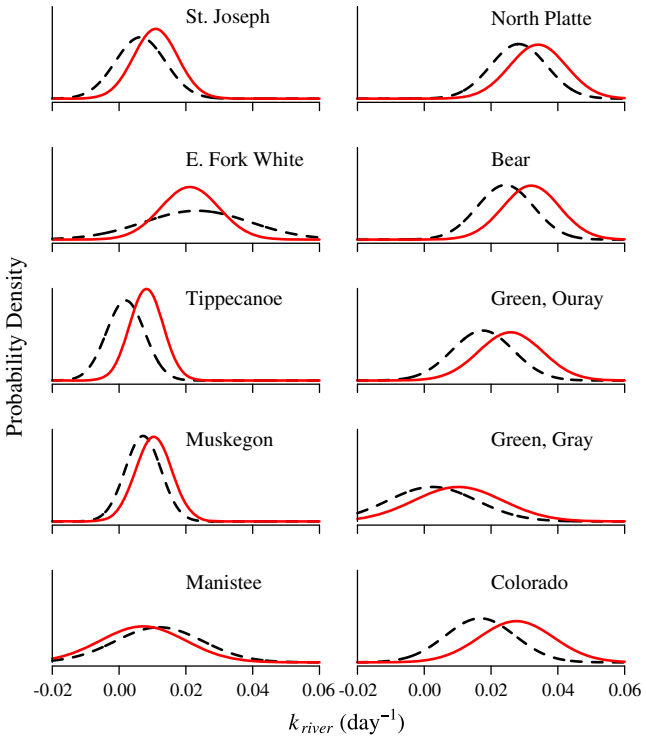

Figure 4. Prior (dashed line) and posterior (solid line) probability distributions for river DOC decay rates with and without glucose. Prior river DOC decay was estimated from posterior distributions of river DOC bioassays by themselves; posterior river DOC decay was estimated from combined river DOC + glucose bioassays to model the potential priming of river DOC by glucose (equation (2)).

Soil leachate decay rates were 7 and 12 times lower than rates from commercial humate (95% HDI = −0.25,−0.03) and glucose (95% HDI = −0.34,−0.17) decay rates at all sites, respectively (Table 3). Mean decay rates for soil leachate were similar to river DOC decay rates (95% HDI = −0.002, 0.02), with mean soil decay rates of 0.001–0.024 and 0.011–0.058 day^{-1} in the Midwestern and western rivers, respectively (Table 3). Nutrient amendments inhibited soil leachate decay in the White and Muskegon Rivers and did not increase soil leachate decay rates at any sites (data not shown). There was no substantial evidence for correlations between soil leachate decay rates and river water chemistry variables (Table 4).

Additions of algal leachate and commercial humate resulted in higher DOC decay rates relative to soil and river DOC alone (Table 3). Algal leachate decay rates were 3 times higher than those for soil leachates (95% HDI = 0.03,0.08), were not nutrient limited (data not shown), and

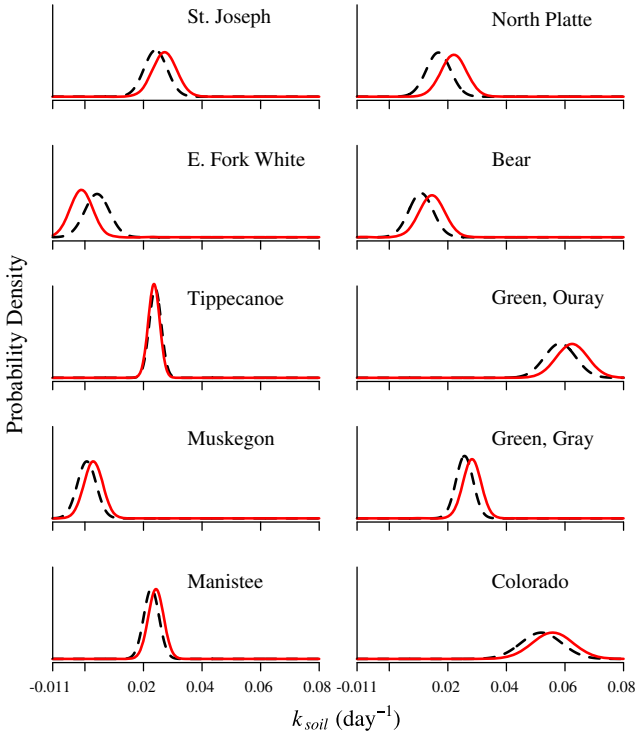

Figure 5. Prior (dashed line) and posterior (solid line) probability distributions for soil leachate decay rates with and without glucose. Prior soil leachate decay was estimated from posterior distributions of soil leachate bioassays by themselves; posterior soil leachate decay was estimated from combined soil + glucose bioassays to model the potential priming of soil leachate by glucose (equation (2)).

ranged from 0.038 to 0.098 day^{-1} in Midwestern rivers (Table 3). There was no evidence for correlations between algal leachate decay rates and water chemistry variables (Table 4). Commercial humate decay ranged from 0.063 to 0.269 day^{-1} in western rivers (Table 3). Decay of commercial humate was strongly positively correlated with river SRP concentrations (Table 4).

3.2. Estimates of Priming Effects

Using the two-compartment DOC decay model (equation (2)), we compared measured and modeled final bioassay DOC concentrations and found that modeled estimates of source-specific decay rates were capable of predicting final DOC concentrations (linear model $r^2 = 0.97$; Figure 2). We used this comparison of measured and modeled final DOC concentrations to validate the modeled decay rates: if the two-compartment decay rate model drastically underestimated or overestimated decay rates, the modeled and measured comparisons would not fall on or near the 1:1 line. We found that modeled bioassay DOC concentrations were less accurate at DOC concentrations above 10 mg C L^{-1} but mostly fell above the 1:1 line, suggesting that modeled decay rate estimates were conservative, as were our estimates of priming effects on more stable DOC uptake (Figure 2).

River DOC, soil leachate, and commercial humate decay was primed by the addition of glucose. The highest modeled priming responses (i.e., where the posterior distribution mean for *k* was higher than prior distribution) were commercial humate incubated with glucose, followed by river DOC with glucose, and soil leachate with glucose (Table 5).

Modeled priming of commercial humate with the addition of glucose was high (Figure 3 and Table 5). The addition of nutrients did not alter the positive priming of commercial humate with glucose (Table 5). Modeled priming of commercial humate by glucose was positively correlated with river turbidity (Table 6).

The addition of glucose positively primed a net mean increase (87%) in river DOC decay rates across all sites, even with slightly negative priming effects at 2 of 10 rivers (Figure 4 and Table 5). The priming effect of river DOC decay with glucose was positive at all sites except the White and Manistee Rivers (Figure 4 and Table 5). Average site-specific priming effects on the decay of river DOC were not correlated with any water chemistry variables (Table 6). Nutrient amendments did not alter the mean priming effect of glucose on river DOC decay (Table 5).

Soil leachate decay rates increased slightly (33%) with the addition of glucose (Figure 5 and Table 5). Bioassay nutrient amendments (N and P) increased mean soil leachate priming effects (Table 5). Algal leachates positively primed soil leachate decay at two of five Midwestern river sites (Figure 6); the overall mean effect of algal leachates on soil leachate decay was also higher with nutrient amendments (Table 5). There was no evidence for correlations between algal priming of soil leachate and river water chemistry (Table 6). In the White River, we found negative priming of soil leachate with added glucose and algal leachates, suggesting an inhibition of soil leachate decay in the presence of more unstable DOC (Figures 5 and 6).

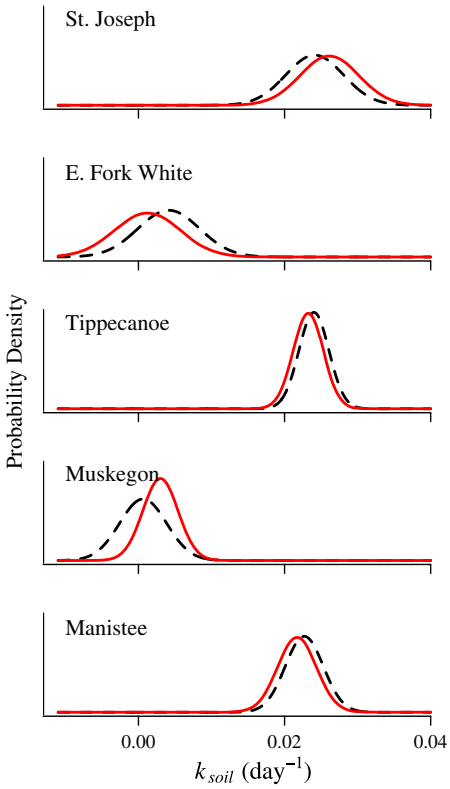

Figure 6. Prior (dashed line) and posterior (solid line) probability distributions for soil leachate decay rates with and without algal leachate. Prior soil leachate decay was estimated from posterior distributions of soil leachate bioassays by themselves; posterior soil leachate decay was estimated from combined soil + algal leachate bioassays to model the potential priming of soil leachate by algal leachate (equation (2)).

4. Discussion

4.1. Assessment of Bayesian Priming Model

Using the Bayesian inverse modeling approach, we detected positive priming effects because (1) testing priming at 5–10 sites allowed for pooled estimates of mean net effects among all sites and (2) using prior information about unstable and more stable DOC decay rates, paired with the Bayesian inverse model, allowed us to estimate two unknown decay rates in a bioassay model characterizing the decay of multiple DOC sources. Most modeled posterior probability distributions for priming of decay rates fell within the same range as those from prior decay rate estimates using bioassays (Figures 3–6) and required pooled effects among sites to detect priming effects (Table 5). We examined the accuracy of our inverse modeling approach by comparing measured and modeled final DOC concentrations from equation (2), where good agreement between measured and modeled DOC confirmed our modeled primed decay rate estimates (Figure 2). We also note that the two-source priming model underestimated the primed decay rates for bioassays with larger DOC concentrations, resulting in higher modeled final DOC concentrations than measured (Figure 2). These high-DOC bioassays were incubations of soil leachates, and because we did not characterize differences in soil leachates, we do not know if the lower predictive power of the model was due to differences in DOC quality, DOC uptake kinetics, or some other variable we did not include in the model. Consequently, while this model performed well for priming tests in bioassays with DOC concentrations below 10 mg C L^{-1}, we are cautious about the use of this model in higher DOC environments without further refinement and testing.

Our approach used simple first-order kinetics to estimate decay rates by assuming DOC decay was a function of the concentration of the DOC pool; this is a common approach for both aquatic and terrestrial OC studies [*Servais et al*., 1989; *Manzoni et al*., 2012]. First-order kinetic models that allowed decay constants to vary with additions of priming substrates better predicted soil C dynamics than single and multiple C pool models [*Neill*, 2011; *Guenet et al*., 2013]. Because we did not measure microbial biomass or composition, we do not know how variation in the microbial assemblage may have contributed to the variation in priming effects at different sites or in different DOC bioassay treatments. We could improve this model by including such microbial assemblage metrics in addition to DOC concentrations, given that microbial structure and function in addition to substrate variability are likely drivers of DOC decay rates. Models describing priming effects that have been developed for soils often include microbial biomass, microbial growth rates and efficiencies, and microbial substrate affinity to incorporate enzyme kinetics in models of DOC uptake and priming [*Neill and Gignoux*, 2006; *Neill and Guenet*, 2010; *Neill*, 2011]. Our focus was to use common bioassay measurements of DOC decay rates to estimate potential priming, but future estimates of priming effects could be improved by including parameters for microbial biomass and growth in addition to varying decay rates with substrate additions.

4.2. Priming of River and Terrestrial DOC Decay

We identified positive priming effects when we added glucose as an unstable DOC source, which subsequently increased river DOC, soil leachate, and commercial humate decay rates in western and Midwestern rivers. Few direct or modeled measurements of the priming effect have been published for

freshwater ecosystems, in strong contrast to the prevalence of priming effect measurements published for terrestrial ecosystems. We modeled positive priming of microbially mediated DOC decay using prior measurements of source-specific DOC decay rates. Without replication of the bioassay treatments within and among rivers, we would not have had enough statistical power to recognize mean positive priming effects in our mixed DOC bioassay treatments (Table 5).

Decay rates of glucose, algal leachates, and commercial humate were higher than decay rates for soil leachate or river DOC alone (Table 3). High uptake of unstable DOC, frequently tested using glucose, is commonly documented in freshwater pelagic and benthic bioassays of DOC decay, regardless of the natural DOC availability [*Ylla et al*., 2012; *Lane et al*., 2013; *Franke et al*., 2013]. Most notably, a whole-stream addition of glucose primed metabolism of bulk stream DOC above ambient rates [*Thouin et al*., 2009]. Bacteria will preferentially consume carbohydrates and protein-like compounds over humics within a larger pool of soil or wetland DOC [*Fellman et al*., 2009; *Berggren et al*., 2010]. We did not account for changes in DOC chemical structure in our bulk measurements of DOC decay rates. In studies comparing biological availability of background DOC with macrophyte and algal leachates as well as terrestrial DOC extracts, bacterial production was higher in incubations with autochthonous and fresh (i.e., recently leached) terrestrial DOC than with bulk DOC [*Farjalla et al*., 2006, 2009]. Measurements of bioassay DOC decay likely underestimate ecosystem-level DOC turnover because bioassay incubations were limited to measuring the decay of DOC left over in river water after the rapid consumption of highly bioavailable DOC [*Pollard*, 2013].

Our model estimates of priming of DOC decay in rivers (both positive and negative) fell within the range of values previously reported for terrestrial and aquatic ecosystems, with site-specific priming responses (calculated from modeled increases in k) for all treatments ranging from −130 to +370% (mean = 35%). Decay rates for soil leachate and river DOC were similar among all 10 sites, but priming effects on river DOC decay were higher than for soil leachate decay (Table 5). Glucose amendments primed an average increase in riparian soil leachate decay of 33% in our study, an effect similar to the 12% increase in soil organic matter mineralization estimated using isotopically labeled glucose and soils from different terrestrial ecosystems by *Guenet et al*. [2014]. While river DOC, soil leachates, and commercial humate decay were highly susceptible to priming by simple sugars, we could not show a significant role of autochthonous DOC in priming soil leachate decay by river microbes (Table 5).

We acknowledge that we did not measure C accumulation in microbial biomass nor mineralization of DOC to CO_2 in our bioassay approach and were limited to measurements of net bulk DOC decay. Our estimates of DOC decay and priming may include "apparent priming": a short-term response to additions of unstable OC where more stable OC is incorporated into living organic pools but is not yet respired. [*Dalenberg and Jager*, 1981; *Kuzyakov et al*., 2000; *Blagodatskaya et al*., 2011]. Because microbial DOC consumption, growth, and respiration remove DOC from the water column, both microbial growth and respiration from DOC are included in our estimates of net bioassay DOC uptake. In soil incubations, real and positive priming effects often emerge after 3 days [*Kuzyakov and Bol*, 2006; *Blagodatskaya et al*., 2011], implying that measured DOC uptake in bioassays longer than 3 days could have represented net mineralization of more stable OC than microbial biomass turnover. We expect that any additional OC uptake into the microbial pool would stimulate microbial DOC consumption and eventually be respired to CO_2 or returned to the available fraction of OC in these rivers.

4.3. Drivers of DOC Decay Rates and Priming

Priming of commercial humate decay by dextrose was positively correlated with river turbidity, suggesting microbial DOC decay in more turbid rivers may have a higher potential for priming of stabile DOC. We found no substantial evidence for correlations between river DOC or soil leachate priming and ambient river water chemistry (Table 6). Nutrient availability can drive patterns of nutrient retention and OC turnover; OC availability may limit microbially mediated heterotrophic nutrient uptake in high-nutrient ecosystems. We found that decay rates of soil and algal leachates were unrelated to background nutrient concentrations, perhaps due to site-specific differences in bioavailability of soil types and species identity of dominant primary producers (Table 4). Nutrient amendments in bioassays did not stimulate decay rates or alter priming effects in most treatments, and in fact, amendments sometimes appeared to inhibit priming compared to bioassay treatments without nutrient amendments (Table 5). Most rivers in our study had high background concentrations of dissolved inorganic N species, and microbial growth was likely more limited by the

availability of OC than inorganic nutrients. Given that other studies show that the amount of priming can be negatively related to nutrient availability, we might expect stronger priming effects in rivers with low nutrient concentrations [*Neff et al*., 2002; *Fontaine et al*., 2004b; *Danger et al*., 2013]. High nutrient concentrations and OC limitation may cause preferential uptake of unstable substrates and a negative priming effect [*Franke et al*., 2013]. Additionally, whether C cycling is more N or P limited may influence priming, as the priming of more stable OC decay may be more prevalent in N-limited ecosystems than in P-limited ecosystems [*Dijkstra et al*., 2013]. In freshwater ecosystems, we expect a range of priming responses depending on complex interactions between OC quality and nutrient availability, as we did for 10 western and Midwestern rivers.

Primary production likely drives the availability of substrates responsible for positive priming in terrestrial and freshwater ecosystems [*Guenet et al*., 2010; *Danger et al*., 2013; *Kuehn et al*., 2014]. That said, we did not see consistent positive priming by algal leachates in soil bioassays, perhaps due to our method of extracting algal DOC, variation in soil type and algal DOC exudation among sites, and lower statistical power with only five rivers used to test this potential priming mechanism (Figure 6). In low-nutrient freshwater microcosm experiments, algae leachates increased rates of leaf litter decomposition by ~20% [*Danger et al*., 2013]. Algal photosynthesis stimulated the growth of microbial decomposers on marsh plant litter, and isotope tracers confirmed the use of algal C by bacteria and fungi [*Kuehn et al*., 2014]. Mixed bacterial incubations with macrophyte and lagoon DOC resulted in higher bacterial growth efficiencies than expected from macrophyte or lagoon DOC incubations alone [*Farjalla et al*., 2009]. In terrestrial ecosystems, rhizosphere exudates primed soil OC mineralization [*Kuzyakov*, 2002; *Bader and Cheng*, 2007; *Dijkstra et al*., 2013]. Future research isolating fresh autochthonous OC for tests of priming effects, perhaps through the use of distinct isotope signatures to trace the fate of unstable and more stable OC pools, is a promising approach for testing in situ drivers of the priming effect in freshwater ecosystems.

There were no obvious shared water chemistry characteristics or trends in single-source DOC decay that explain why soil or river DOC decay was positively primed by glucose or algal leachates in most rivers but was negatively primed in others. We found negative priming in 2 of 10 rivers: the Manistee River (Figures 4 and 6) and the East Fork White River (Figures 5 and 6). Both rivers are in the Midwestern United States but did not have similar levels of nutrient pollution, turbidity, or agricultural land use. Analyses of microbial assemblage structure as well as soil, algal, and river DOC chemical structure may have identified differences in the Manistee and East Fork White relative to the other rivers.

5. Conclusions

Once transported from soils to freshwater ecosystems, terrestrial OC is available for microbial consumption, reflected in studies that show respiration of old (>1000 years) OC in freshwater ecosystems [*Caraco et al*., 2010; *McCallister and del Giorgio*, 2012] and contributions of terrestrial OC to freshwater food webs [*Polis et al*., 1997; *Carpenter et al*., 2005; *Marcarelli et al*., 2011]. Increasing microbial decay of more stable OC, due to a positive priming effect, may be partially responsible for the rapid breakdown of terrestrial OC in freshwater ecosystems. We found strong evidence for positive priming in the decay of river DOC, soil leachate, and commercial humate in the presence of glucose and river microbes, a process not previously quantified in rivers. Future measurements and models of priming effects, in additional ecosystems with varying nutrient regimes and diverse primary producers and microbial assemblages, will clarify the mechanisms driving high rates of terrestrial OC processing in freshwater ecosystems.

Acknowledgments

We thank A. L. Saville, C. F. Johnson, J. D. Reed, and the rest of the river gypsies for support in the field and laboratory. Comments from E. Pendall, M. Clementz, P. Colberg, and D. Williams greatly improved this manuscript. This research was funded by the National Science Foundation (DEB0921598) and an Arts and Sciences Independent Study Award from the University of Wyoming. Data from this paper are available from E.R. Hotchkiss upon request.

References

Alvarez-Cobelas, M., D. G. Angeler, S. Sanchez-Carrillo, and G. Almendros (2011), A worldwide view of organic carbon export from catchments, *Biogeochemistry*, doi:10.1007/s10533-010-9553-z.

Amado, A. M., V. F. Farjalla, F. A. Esteves, R. L. Bozelli, F. Roland, and A. Enrich-Prast (2006), Complementary pathways of dissolved organic carbon removal pathways in clear-water Amazonian ecosystems: Photochemical degradation and bacterial uptake, *FEMS Microbiol. Ecol.*, *56*, 8–17, doi:10.1111/j.1574-6941.2006.00028.x.

Aufdenkampe, A. K., E. Mayorga, P. A. Raymond, J. M. Melack, S. C. Doney, S. R. Alin, R. E. Aalto, and K. Yoo (2011), Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere, *Front. Ecol. Environ.*, *9*, 53–60, doi:10.1890/100014.

Bader, N. E., and W. Cheng (2007), Rhizosphere priming effect of Populus fremontii obscures the temperature sensitivity of soil organic carbon respiration, *Soil Biol. Biochem.*, *39*, 600–606, doi:10.1016/j.soilbio.2006.09.009.

Baines, S. B., and M. L. Pace (1991), The production of dissolved organic matter by phytoplankton and its importance to bacteria: Patterns across marine and freshwater systems, *Limnol. Oceanogr.*, *36*, 1078–1090.

Battin, T. J., L. A. Kaplan, S. Findlay, C. S. Hopkinson, E. Marti, A. I. Packman, J. D. Newbold, and F. Sabater (2008), Biophysical controls on organic carbon fluxes in fluvial networks, *Nat. Geosci.*, *1*, 95–100, doi:10.1038/ngeo101.

Berggren, M., H. Laudon, M. Haei, L. Ström, and M. Jansson (2010), Efficient aquatic bacterial metabolism of dissolved low-molecular-weight compounds from terrestrial sources, *ISME J.*, *4*, 408–416, doi:10.1038/ismej.2009.120.

Bianchi, T. S. (2011), The role of terrestrial derived organic carbon in the coastal ocean: A changing paradigm and the priming effect, *Proc. Natl. Acad. Sci. U.S.A.*, *108*, 19,473–19,481, doi:10.1073/pnas.1017982108.

Bingeman, C. W., J. E. Varner, and W. P. Martin (1952), The effect of the addition of organic materials on the decomposition of an organic soil, *Proc. Soil Sci. Am.*, *17*, 34–38, doi:10.2136/sssaj1953.03615995001700010008x.

Blagodatskaya, E., T. Yuyukina, S. Blagodatsky, and Y. Kuzyakov (2011), Three-source-partitioning of microbial biomass and of CO_2 efflux from soil to evaluate mechanisms of priming effects, *Soil Biol. Biochem.*, *43*, 778–786, doi:10.1016/j.soilbio.2010.12.011.

Brandt, L. A., J. Y. King, S. E. Hobbie, D. G. Milchunas, and R. L. Sinasbaugh (2010), The role of photodegradation in surface litter decomposition across a grassland ecosystem precipitation gradient, *Ecosystems*, *13*, 765–781, doi:10.1007/s10021-010-9353-2.

Caraco, N., J. E. Bauer, J. J. Cole, S. Petsch, and P. Raymond (2010), Millennial-aged organic carbon subsidies to a modern river food web, *Ecology*, *91*, 2385–2393, doi:10.1890/09-0330.1.

Carpenter, S. R., J. J. Cole, M. L. Pace, M. Van de Bogert, D. L. Bade, D. Bastviken, C. M. Gille, J. R. Hodgson, J. F. Kitchell, and E. S. Kritzberg (2005), Ecosystem subsidies: Terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes, *Ecology*, *86*, 2737–2750, doi:10.1890/04-1282.

Cole, J. J., and N. F. Caraco (2001), Carbon in catchments: Connecting terrestrial carbon losses with aquatic metabolism, *Mar. Freshwater Res.*, *52*, 101–110, doi:10.1071/MF00084.

Cole, J. J., G. E. Likens, and D. L. Strayer (1982), Photosynthetically produced dissolved organic carbon: An important carbon source for planktonic bacteria, *Limnol. Oceanogr.*, *27*, 1080–1090.

Cole, J. J., et al. (2007), Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget, *Ecosystems*, *10*, 171–184, doi:10.1007/s10021-006-9013-8.

Cole, J. J., S. R. Carpenter, J. Kitchell, M. L. Pace, C. T. Solomon, and B. Weidel (2011), Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen, *Proc. Natl. Acad. Sci. U.S.A.*, *108*, 1975–1980, doi:10.1073/pnas.1012807108.

Dalenberg, J. W., and G. Jager (1981), Priming effects of small glucose additions to ^{14}C-labelled soil, *Soil Biol. Biochem.*, *13*, 219–223, doi:10.1016/0038-0717(81)90024-9.

Danger, M., J. Cornut, E. Chauvet, P. Chavez, A. Elger, and A. Lecerf (2013), Benthic algae stimulate leaf litter decomposition in detritus-based headwater streams: a case of aquatic priming effect?, *Ecology*, *94*, 1604–1613, doi:10.1890/12-0606.1.

De Lange, H. J., D. P. Morris, and C. E. Williamson (2003), Solar ultraviolet photodegradation of DOC may stimulate freshwater food webs, *J. Plankton Res.*, *25*, 111–117, doi:10.1093/plankt/25.1.111.

Dijkstra, F. A., Y. Carrillo, E. Pendall, and J. A. Morgan (2013), Rhizosphere priming: A nutrient perspective, *Front. Microbiol.*, *4*, 216, doi:10.3389/fimb.2013.00216.

Duarte, C. M., and Y. T. Prairie (2005), Prevalence of heterotrophic and atmospheric CO_2 emissions from aquatic ecosystems, *Ecosystems*, *8*, 862–870, doi:10.1007/s10021-005-0177-4.

Farjalla, V. F., D. A. Azevedo, F. A. Esteves, R. L. Bozelli, F. Roland, and A. Enrich-Prast (2006), Influence of hydrological pulse on bacterial growth and DOC uptake in a clear-water Amazonian lake, *Microb. Ecol.*, *52*, 334–344, doi:10.1007/s00248-006-9021-4.

Farjalla, V. F., C. C. Marinho, B. M. Faria, A. M. Amado, F. de A. Esteves, R. L. Bozelli, and G. Giroldo (2009), Synergy of fresh and accumulated organic matter to bacterial growth, *Microb. Ecol.*, *57*, 657–666, doi:10.1007/s00248-008-9466-8.

Fellman, J. B., E. Hood, R. T. Edwards, and J. B. Jones (2009), Uptake of allochthonous dissolved organic matter from soil and salmon in coastal temperate rainforest streams, *Ecosystems*, *12*, 747–759, doi:10.1007/s10021-009-9254-4.

Fisher, S. G., and G. E. Likens (1973), Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism, *Ecol. Monogr.*, *43*, 421–439, doi:10.2307/1942301.

Fontaine, S., A. Mariotti, and L. Abbadie (2003), Priming effect of organic matter: A question of microbial competition?, *Soil Biol. Biochem.*, *35*, 837–843, doi:10.1016/S0038-0717(03)00123-8.

Fontaine, S., G. Bardoux, D. Benest, B. Verdier, A. Mariotti, and L. Abbadie (2004a), Mechanisms of the priming effect in a savannah soil amended with cellulose, *Soil Sci. Soc. Am. J.*, *68*, 125–131, doi:10.2136/sssaj2004.0125.

Fontaine, S., G. Bardoux, L. Abbadie, and A. Mariotti (2004b), Carbon input to soil may decrease soil carbon content, *Ecol. Lett.*, *7*, 314–320, doi:10.1111/j.1461-0248.2004.00579.x.

Franke, D., E. J. Bonnell, and S. E. Ziegler (2013), Mineralisation of dissolved organic matter by heterotrophic stream biofilm communities in a large boreal catchment, *Freshwater Biol.*, *58*, 2007–2026, doi:10.1111/fwb.12187.

Guenet, B., M. Danger, L. Abbadie, and G. Lacroix (2010), Priming effect: Bridging the gap between terrestrial and aquatic ecology, *Ecology*, *91*, 2850–2861, doi:10.1890/09-1968.1.

Guenet, B., T. Eglin, N. Vasilyeva, P. Peylin, P. Ciais, and C. Chenu (2013), The relative importance of decomposition and transport mechanisms in accounting for soil organic carbon profiles, *Biogeosciences*, *10*, 2379–2392, doi:10.5194/bg-10-2379-2013.

Guenet, B., M. Danger, L. Harrault, B. Allard, M. Jauset-Alcala, G. Bardoux, D. Benest, L. Abbadie, and G. Lacroix (2014), Fast mineralization of land-born C in inland waters: First experimental evidence of aquatic priming effect, *Hydrobiologia*, *721*, 35–44, doi:10.1007/s10750-013-1635-1.

Guillemette, F., S. L. McCallister, and P. A. del Giorgio (2013), Differentiating the degradation dynamics of algal and terrestrial carbon within complex natural dissolved organic carbon in temperate lakes, *J. Geophys. Res. Biogeosci.*, *118*, 963–973, doi:10.1002/jgrg.20077.

Hall, R. O., G. E. Likens, and H. L. Malcom (2001), Trophic basis of invertebrate production in 2 streams at the Hubbard Brook Experimental Forest, *J. North Am. Soc.*, *20*, 432–447, doi:10.2307/1468040.

Hilborn, R., and M. Mangel (1997), *The Ecological Detective. Confronting Models with Data*, Princeton Univ. Press, Princeton, N. J.

Kruschke, J. K. (2013), Bayesian estimation supersedes the *t* test, *J. Exp. Psych. Gen.*, *142*, 573–603, doi:10.1037/a0029146.

Kuehn, K. A., S. N. Francoeur, R. H. Findlay, and R. K. Neely (2014), Priming in the microbial landscape: Periphytic algal stimulation of litter-associated microbial decomposers, *Ecology*, *95*, 749–762, doi:10.1890/13/0430/1.

Kuzyakov, Y. (2002), Review: Factors affecting rhizosphere priming effects, *J. Plant Nutr. Soil Sci.*, *165*, 382–396, doi:10.1002/1522-2624(200208)165:4<382::AID-JPLN382>3.0.CO;2-#.

Kuzyakov, Y. (2010), Priming effects: Interactions between living and dead organic matter, *Soil Biol. Biochem.*, *42*, 1363–1371, doi:10.1016/j.soilbio.2010.04.003.

Kuzyakov, Y., and R. Bol (2006), Sources and mechanisms of priming effect induced in two grassland soils amended with slurry and sugar, *Soil Biol. Biochem.*, *38*, 747–758, doi:10.1016/j.soilbio.2005.06.025.

Kuzyakov, Y., J. K. Friedel, and K. Stahr (2000), Review of mechanisms and quantification of priming effects, *Soil Biol. Biochem.*, *32*, 1485–1498, doi:10.1016/S0038-0717(00)00084-5.

Lane, C. S., D. R. Lyon, and S. E. Ziegler (2013), Cycling of two carbon substrates of contrasting lability by heterotrophic biofilms across a nutrient gradient of headwater streams, *Aquat. Sci.*, *75*, 235–250, doi:10.1007/s00027-012-0269-0.

Link, W. A., and M. J. Eaton (2012), On thinning of chains in MCMC, *Meth. Ecol. Evol.*, *3*, 112–115, doi:10.1111/j.2041-210X.2011.00131.x.

Lutz, B. D., E. S. Bernhardt, B. J. Roberts, R. M. Cory, and P. J. Mulholland (2012), Distinguishing dynamics of dissolved organic matter components in a forested stream using kinetic enrichments, *Limnol. Oceanogr.*, *57*, 76–98, doi:10.4319/lo.2012.57.1.0076.

Manzoni, S., G. Piñeiro, R. B. Jackson, E. G. Jobbágy, J. H. Kim, and A. Porporato (2012), Analytical models of soil and litter decomposition: Solutions for mass loss and time-dependent decay rates, *Soil Biol. Biochem.*, *50*, 66–76, doi:10.1016/j.soilbio.2012.02.029.

Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall (2011), Quantity and quality: Unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters, *Ecology*, *92*, 1215–1225, doi:10.1890/10-2240.1.

McCallister, S. L., and P. A. del Giorgio (2012), Evidence for the respiration of ancient terrestrial organic C in northern temperate lakes and streams, *Proc. Natl. Acad. Sci. U.S.A.*, *109*, 16,963–16,968, doi:10.1073/pnas.1207305109.

Meredith, M., and J. Kruschke (2013), BEST: Bayesian estimation supersedes the *t*-Test, R package version 0.2.0. [Available at http://cran.r-project.org/web/packages/BEST/.]

Moran, M. A., and R. G. Zepp (1997), Role of photoreactions in the formation of biologically labile compounds from dissolved organic matter, *Limnol. Oceanogr.*, *42*, 1307–1316.

Neff, J. C., A. R. Townsend, G. Gleixner, S. J. Lehman, J. Turnbull, and W. D. Bowman (2002), Variable effects of nitrogen additions on the stability and turnover of soil carbon, *Nature*, *419*, 915–917, doi:10.1038/nature01136.

Neill, C. (2011), Impacts of crop residue management on soil organic matter stocks: A modeling study, *Ecol. Modell.*, *222*, 2751–2760, doi:10.1016/j.ecolmodel.2011.04.029.

Neill, C., and J. Gignoux (2006), Soil organic matter decomposition driven by microbial growth: A simple model for a complex network of interactions, *Soil Biol. Biochem.*, *38*, 803–811, doi:10.1016/j.soilbio.2005.07.007.

Neill, C., and B. Guenet (2010), Comparing two mechanistic formalisms for soil organic matter dynamics: A test with in vitro priming effect observations, *Soil Biol. Biochem.*, *42*, 1212–1221, doi:10.1016/j.soilbio.2010.04.016.

Plummer, M. (2013), Rjags: Bayesian graphical models using MCMC, R package version 3-10. [Available at http://cran.r-project.org/web/packages/rjags/.]

Polis, G. A., W. B. Anderson, and R. D. Holt (1997), Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs, *Annu. Rev. Ecol. Syst.*, *28*, 289–316, doi:10.1146/annurev.ecolsys.28.1.289.

Pollard, P. C. (2013), In situ rapid measures of total respiration rate capture the super labile DOC bacterial substrates of freshwater, *Limnol. Oceanogr. Methods*, *11*, 584–593, doi:10.4319/lom.2013.11.584.

R Core Team (2012), *R: A language and Environment for Statistical Computing, Reference Index 2.15.2*, R Foundation for Statistical Computing, Vienna. [Available at http://www.R-project.org/.]

Raymond, P. A., et al. (2013), Global carbon dioxide emissions from inland waters, *Nature*, *503*, 355–359, doi:10.1038/nature12760.

Schlesinger, W. H., and J. M. Melack (1981), Transport of organic carbon in the world's rivers, *Tellus*, *33*, 172–187, doi:10.1111/j.2153-3490.1981.tb01742.x.

Servais, P., A. Anzil, and C. Ventresque (1989), Simple method for determination of biodegradable dissolved organic carbon in water, *Appl. Environ. Microbiol.*, *55*, 2732–2734.

Thouin, J. A., W. M. Wollheim, C. J. Vörösmarty, J. M. Jacobs, and W. H. McDowell (2009), The biogeochemical influences of NO_3^-, dissolved O_2, and dissolve organic C on stream NO_3^- uptake, *J. North Am. Soc.*, *28*, 894–907, doi:10.1899/08-183.1.

Ward, N. D., R. G. Keil, P. M. Medeiros, D. C. Brito, A. C. Cunha, T. Dittmar, P. L. Yager, A. V. Krusche, and J. E. Richey (2013), Degradation of terrestrial derived macromolecules in the Amazon River, *Nat. Geosci.*, *6*, 530–533, doi:10.1038/ngeo1817.

Wetzel, R. G., P. G. Hatcher, and T. S. Bianchi (1995), Natural photolysis by ultraviolet irradiance of recalcitrant organic matter to simple substrates for rapid bacterial metabolism, *Limnol. Oceanogr.*, *40*, 1369–1380.

Wetzels, R. G., and E.-J. Wagenmakers (2012), A default Bayesian hypothesis test for correlations and partial correlations, *Psychon. Bull. Rev.*, *19*, 1057–1064, doi:10.3758/s13423-012-0295-x.

Ylla, I., A. M. Romaní, and S. Sabater (2012), Labile and recalcitrant organic matter utilization by river biofilm under increasing water temperature, *Microb. Ecol.*, *64*, 593–604, doi:10.1007/s00248-012-0062-6.