Variability of heterotrophic metabolism in small stream corridors of an early successional watershed

Variability of heterotrophic metabolism in small stream corridors of an early successional watershed

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[1] Metabolic activity in stream corridors is regulated by a complex combination of factors that are difficult to disentangle in mature ecosystems. Chicken Creek in Germany, an experimentally created watershed in an early successional stage, offers the opportunity to assess the spatiotemporal variation in metabolic activity in a simplified system. We measured microbial respiration in soils and sediments along the hydrologic flow path from upland terrestrial to ephemeral to perennial sites of three stream corridors. Dry soils and sediments were rewetted before respiration measurements to mimic periods of activity during and after rainfall. Respiration rates and organic matter contents of soil and sediment were generally low. The presence of algae and accretion of vascular plant fragments in the perennial stream reaches increased respiration rates, pointing to the importance of particulate organic matter. Contrary to expectation, respiration rates of rewetted soil and sediment from dry stream channels were similar to rates measured with sediments collected in the perennial channel sections. This suggests that permanent water availability was not a main factor determining metabolic potential in the early successional Chicken Creek watershed. Carbon turnover in perennial channels was fourfold to eightfold higher than in ephemeral channels and terrestrial sites, as water was permanently available. However, this magnitude was insufficient for perennial channels to compensate for the large surface area of terrestrial soils: extrapolated to a year and the whole watershed, stream channels contributed only 5% to total carbon turnover, 95% being due to soils during and after rainfall events.

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1. Introduction

[2] Landscapes are characterized by patchiness of physical and biological attributes [*Winemiller et al.*, 2010; *Moore et al.*, 2009], which influence biogeochemical processes and whole-ecosystem metabolism [*Malard et al.*, 2002]. As a result, rates of biogeochemical processes are often highly variable across landscapes, particularly at terrestrial-aquatic interfaces and along hydrologic flow paths, from upland sites to streams and longitudinally within stream networks [*Larned et al.*, 2010; *Sponseller and Fisher*, 2006]. Landscape patches showing disproportionately high reaction rates relative to the surrounding matrix have been termed hot spots of metabolic activity [*McClain et al.*, 2003]. They are typically found at interfaces where complementary reactants meet because different flow paths converge. Such hot spots can occur along gradients of redox potential [*Mitchell and Branfireun*, 2005] or in the hyporheic zone of streams where groundwater and stream water mix [*Mulholland et al.*, 1997; *Boulton et al.*, 2010].

[3] Variation in metabolic activity along hydrologic flow paths in riverine landscapes is well documented. For example, high primary production and nitrate uptake rates have been described at outwelling sandbar edges where nutrient-rich groundwater and light availability enable intense photosynthetic activity [*Valett et al.*, 1994]. If enriched with dissolved organic carbon (DOC), upwelling groundwater can provide an important carbon and energy source also for heterotrophic stream microbes [*Jones et al.*, 1995; *Boulton et al.*, 2010]. Similarly, elevated hyporheic respiration rates have been observed in downwelling areas of streams, indicating that algal primary production at the surface can provide labile organic matter on which hyporheic microbes capitalize to boost their metabolism [*Jones et al.*, 1995]. Thus, both upward and downward vertical water exchange can enhance metabolic activities in stream sediments by supplying essential resources for microbial metabolism.

[4] Besides DOC, particulate organic matter (POM) plays an important role in fueling microbial activity in streams. Sources of POM can be allochthonous, consisting mainly of

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litter derived from riparian vegetation, or autochthonous, originating from in-stream vascular plants, algae or other organisms. Although litter input from riparian trees is the most important source of POM in woodland streams [*Webster and Meyer*, 1997], watersheds in early successional stages have scarce upland [*Chapin et al.*, 1994] and riparian vegetation [*Milner and Robertson*, 2010]. This leads to low POM availability and resource heterogeneity caused by isolated plant and litter patches.

[5] Heterotrophic metabolic activity in ecosystems can be assessed by measuring community respiration as an integrative process that reflects oxygen-dependent metabolism and, in aerobic environments, accounts for the bulk of CO_2 flux to the atmosphere [*Young et al.*, 2008; *Martin and Bolstad*, 2009]. Quantity and quality of organic matter, temperature, nutrient availability, redox potential and the physical structure of soils and sediments are all important factors influencing rates of respiration in soils and sediments [e.g., *Hedin*, 1990; *Koutný and Rulík*, 2007; *Arevalo et al.*, 2010; *Bond-Lamberty and Thomson*, 2010]. However, the main driver is often water availability, especially in arid and semiarid climates [*Noy-Meir*, 1973; *Belnap et al.*, 2005] where occasional precipitation events create pulses of metabolic activity in soils and sediments of ephemeral stream channels [*Sala and Lauenroth*, 1982; *Belnap et al.*, 2005; *Sponseller*, 2007]. Such increases in activity after precipitation events are considered hot moments [*Belnap et al.*, 2005; *Harms and Grimm*, 2008]. Similar to hot spots, hot moments have been defined as short periods when biogeochemical reaction rates are substantially increased compared to the intervening periods of low activity [*McClain et al.*, 2003]. They are often related to water availability. For example, growth and abundance of bacteria in sediments of ephemeral Mediterranean streams have been found to depend strongly on moisture availability and to cease instantly when sediments desiccate [*Amalfitano et al.*, 2008; *Marxsen et al.*, 2010]. Likewise, marked reductions of microbial growth and soil respiration rates have been described with decreasing soil water content [e.g., *Cook and Orchard*, 2008]. This suggests elevated microbial activity in stream sediments at sites with permanent water.

[6] Metabolic activity in mature ecosystems is regulated by a complex combination of factors that can be difficult to disentangle. However, physically and biologically simple model systems such as landscapes recently formed by volcanism [*Vitousek*, 2004] or glacier recession [*Milner et al.*, 2007] with low structural heterogeneity, simple food webs, low input of allochthonous organic matter, and no legacy of human use provide opportunities to assess activity patterns and their causes at the landscape scale. Alternatively, artificially created watersheds subject to natural colonization and development from an initially bare stage can be used to study processes occurring during early ecosystem succession [*Gerwin et al.*, 2009]. Surface runoff in such scarcely vegetated landscapes leads to rapid erosion especially of soft substrates, and formation of a network of rills and both ephemeral and perennial stream channels [*Graf*, 1988]. The resulting drainage network includes sites experiencing variable water availability and disturbance by scour and fill, which influence primary production and other ecosystem processes [*Stanley et al.*, 2010]. These gradients of water availability and disturbance, together with broadly homogenous substrates and scarce vegetation, make early successional watersheds suitable to distinguish places (i.e., landscape structures) and times of intense metabolic activity.

[7] Taking advantage of an experimental watershed constructed in 2005 [*Gerwin et al.*, 2009] we investigated patterns of metabolic activity and their potential causes at the landscape scale. The objectives of the study were to determine respiration rates in soil and sediment along hydrologic flow paths within small stream corridors of this watershed in an early successional stage. We hypothesized that permanent water availability and the quantity and quality of organic matter would be the main drivers of microbial respiration. Specifically, we explored five expectations: (1) Soil from terrestrial upland sites and sediments from ephemeral channel sections will have low potential metabolic activity after rewetting compared to permanently wet or moist sediments from perennial stream sections. (2) Metabolic activity after rewetting will be higher in ephemeral stream sections than in adjacent terrestrial soil because physically sheltered and less hydrophobic sediments retain moisture longer after rainfall than upland soils. (3) Metabolic activity will decrease within perennial stream sections from upwelling to downwelling sites to sites with perched surface flow due to differences in carbon and nutrient supply. (4) Metabolic activity will be higher at permanently submerged sites than at adjacent parafluvial sites because of better vertical water exchange and nutrient delivery. (5) Metabolic activities at places where water is permanently available will play a notable role in whole-system carbon flux to the atmosphere in spite of the small spatial extent of these places.

2. Material and Methods

2.1. Study Site

[8] The study was conducted in an experimental watershed (dubbed Chicken Creek watershed) located in eastern Germany near the city of Cottbus about 150 km southeast of Berlin (51°36′N, 14°16′E). Average annual precipitation in the area is 559 mm and average air temperature is 9.3°C (period 1971–2000; Meteorological Station Cottbus, Deutscher Wetterdienst). The Chicken Creek watershed was created in 2004 and 2005 by depositing a 2–4 m layer of Pleistocene sands on top of a 1–2 m impervious layer of Tertiary clay forming a shallow basin [*Gerwin et al.*, 2009]. The watershed of 6 ha (400 m × 150 m) has a water storage volume (aquifer) of 117,500 m^3. The total elevational difference is about 15 m along the main axis, resulting in an average slope of 3.5%. Geomorphology and biological colonization of the watershed have undergone an unrestricted natural development from the initially bare stage.

[9] Between November 2007 and October 2008, the watershed was sparsely covered by vegetation consisting primarily of forbs. The main species was Canadian horseweed (*Conyza canadensis* (L.) Cronquist), although some grasses, especially Wood small reed (*Calamagrostis epigejos* (L.) Roth) and scattered woody plants such as Scots pine (*Pinus sylvestris* L.), Goat willow (*Salix caprea* L.) and Black locust (*Robinia pseudoacacia* L.) were also present. Within 2 years, the initially plane surface of the watershed had been shaped by water erosion, resulting in a well-developed network of rills and channels. The three main channels each drain separate portions of the watershed into a small pond

Table 1. Physical and Chemical Characteristics of the Three Mainstream Corridors in the Chicken Creek Watershed[a]

Parameter	Stream 1	Stream 2	Stream 3
Watershed area (m^2)	950	7473	20496
Mean discharge ($L\ s^{-1}$)	0.02	0.13	0.37
Length of perennial stream section (m)	20	38	43
Length of ephemeral stream channel (m)	103	171	249
Permanently wetted streambed area (m^2)	4	99	68
Ephemeral streambed area (m^2)	30	390	432
Channel slope (%)	6.5	5.1	3.9
Channel width at ground level (m)	1.2 (0.6–1.9)	2.6 (1.0–5.8)	2.2 (0.2–5.4)
Surface water DON ($\mu g\ N\ L^{-1}$)	18.1 ± 5.9	18.6 ± 5.0	41.6 ± 11.9
Pore water DON ($\mu g\ N\ L^{-1}$)	17.4 ± 5.0	24.3 ± 7.2	34.4 ± 13.4
Rainwater DON ($mg\ N\ L^{-1}$)		4.0 ± 0.8	
Surface water NH_4^+ ($\mu g\ N\ L^{-1}$)	115.6 ± 25.5	74.4 ± 9.5	146.4 ± 32.7
Pore water NH_4^+ ($\mu g\ N\ L^{-1}$)	97.8 ± 10.1	62.4 ± 2.5	121.7 ± 38.9
Rainwater NH_4^+ ($mg\ N\ L^{-1}$)		2.2 ± 0.3	
Surface water PO_4^{3-} ($\mu g\ P\ L^{-1}$)	4.3 ± 0.6	4.1 ± 0.3	6.2 ± 0.5
Pore water PO_4^{3-} ($\mu g\ P\ L^{-1}$)	5.9 ± 1.3	4.9 ± 0.6	7.5 ± 1.6
Rainwater PO_4^{3-} ($\mu g\ P\ L^{-1}$)		6.5	
Surface water DOC ($mg\ L^{-1}$)	16.3 ± 0.8	11.2 ± 0.7	15.9 ± 1.1
Pore water DOC ($mg\ L^{-1}$)	18.3 ± 0.9	10.8 ± 0.6	14 ± 0.5
Rainwater DOC ($mg\ L^{-1}$)		2.5 ± 0.2	

[a]Data on the stream channels refer to the main stems of the drainage networks. Rainwater samples were collected at a single site. Note different unit for N species in rainwater. Values are means ± 1SE with ranges in parentheses.

just downstream. The upper portions of the channel network were ephemeral, while upwelling groundwater at a subterranean clay dam downstream created a short perennial section of permanent surface flow in all of the three main channels of the watershed (Table 1). Only part of the channel width was submerged under base flow conditions, but the parafluvial sediment always remained water saturated, because elevational differences between the water table and the parafluvial ground surface level were minor (1–5 cm). Most precipitation events of more than 1 mm led to surface runoff and expansion of the wetted channel portions. As a result, surface flow connected the ephemeral upstream sections to the perennial downstream sections for 101 days during the sampling year, as inferred from water level monitoring in the pond downstream.

2.2. Sampling Procedures and Field Measurements

[10] We took advantage of the three mainstream corridors in the Chicken Creek watershed to analyze soils and sediments at sites with distinct characteristics along the hydrologic flow path. Specifically, eight sites differing in hydrological characteristics were selected along each of the stream channels (Figure 1): (1) a terrestrial upland site, (2) an upstream ephemeral channel site adjacent to the terrestrial site and submerged only during major rain events, (3) an upwelling site of the perennial channel section downstream, (4) a parafluvial site adjacent to the upwelling site, (5) a site in the perennial channel section with perched flow, (6) a parafluvial site adjacent to the site with perched flow, (7) a downwelling site, and (8) a parafluvial site adjacent to the downwelling site. We collected all samples during 1 week periods in the winter (end of November, occasional night frosts) of 2007 and in the spring (April), summer (August), and autumn (early October) of 2008. Upstream reaches with ephemeral water flow were always sampled when dry.

[11] We took three replicate samples of surface soil or sediment (top 2 cm) at each site, resulting in a total of 288 samples (3 channels × 8 sites × 3 replicates × 4 seasons). Replicate samples at each site were taken at about 10 cm distance. Each of them consisted of 8 pooled cores taken with a syringe (2.8 cm inner diameter, lower end cut off)

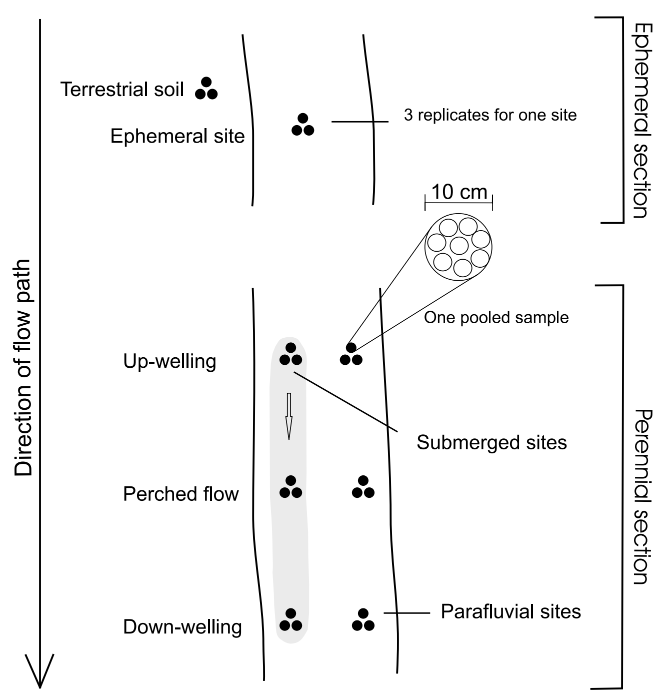

Figure 1. Sampling design used for each of the three mainstream corridors of the Chicken Creek watershed. A total of eight types of samples were taken in each stream corridor: upland terrestrial soil, sediment from the ephemeral stream sites, and sediment from six additional wet or moist (parafluvial) sites in the perennial stream sections.

within a circular surface area of 78.5 cm^2. Subsamples were taken for respiration, organic matter and carbohydrate analyses (see below). Before extracting the cores for these pooled samples, we took additional cores within the same area to determine total pore volume and chlorophyll *a*. A 10 mL syringe with the lower end cut off was used to obtain undisturbed cores (1.5 cm inner diameter, 2 cm depth) for pore volume determinations. A 2 mL syringe (1.0 cm inner diameter) with the lower end cut off was used to collect two pooled soil or sediment samples (2 × 1 mL, total surface area of 1.57 cm^2), which were immediately placed in brown glass bottles containing 8 mL of 90% ethanol and stored in the dark for later chlorophyll analysis.

2.3. Community Respiration, Organic Matter, Carbohydrates, and Chlorophyll

[12] Community respiration captured all organisms associated with the sand grains in soil and sediment. It was measured as oxygen consumption in a flowthrough laboratory system at constant temperature (10°C in winter, 15°C in spring and autumn, 18°C in summer) within 12 h after sampling. The flow rate was normally set at 0.1–0.2 mL min^{-1} to mimic flow conditions in the field. When oxygen consumption was high, flow rate was occasionally increased to up to 0.36 mL min^{-1}. Prior trials showed that the relationship between flow rate and oxygen consumption was linear under these conditions. Samples from perennial reaches were percolated with surface water from the respective channel. Rainwater obtained from rain samplers in the Chicken Creek watershed was used for sediments from the ephemeral reaches and upland soil to simulate the effect of precipitation events on respiratory activity at these sites. Six respiration chambers filled with sediment were simultaneously monitored together with an additional control chamber containing either stream or rainwater only. The chambers used for measuring respiration were glass syringes (10 or 20 mL volume) sealed at the top end by a rubber stopper in which an oxygen optode microsensor (Microx TX3, PreSens GmbH, Regensburg, Germany) was inserted. Chambers were connected to a peristaltic pump (ISMATEC Ecoline, Glattbrugg, Switzerland) controlling flow rate and placed in a water bath for temperature control. Measurements were started after water in the sediment chamber had once been completely replaced and flow rate and oxygen consumption rates were stable. This took between 20 and 60 min, depending on the flow rate and syringe volume. Five measurements were then taken per sample every 3 min and the mean was used for further analysis. After the respiration measurements, samples were dried at 105°C to constant weight and combusted in a muffle furnace (3h at 430°C) to determine total dry mass (DM) and organic matter (OM) content.

[13] Effects of dissolved nutrients and carbon sources on community respiration were determined at one occasion in August 2008 when plant biomass was highest in the watershed. Sediment was collected from all three streams at the sites with perched flow. Respiration was measured in subsamples of this sediment percolated either with stream water from the watershed containing natural DOC or with a mineral nutrient solution in deionized water (1.62 mM $NaNO_3$ and 0.106 mM KH_2PO_4). Particulate organic matter (POM) that was loosely associated with sediment [*Pusch and Schwoerbel*, 1994] was removed from a third sediment subsample by thoroughly rinsing with 400 mL of water. Subsequently, this subsample was also percolated with mineral nutrient solution.

[14] We measured total carbohydrate content in sediments as a proxy for extracellular polymeric substances (EPS), which are indicative of microbial biofilm development. Samples for carbohydrate analysis were frozen in liquid nitrogen within 8 h after sampling and stored at −20°C. Carbohydrate content was later estimated in thawed samples by the phenol-sulphuric acid method [*DuBois et al.*, 1956] with slight modifications. Briefly, 2 mL of deionized water and 50 μL of aqueous phenol (80%) were added to 60–80 mg fresh weight of soil or sediment before mixing the solution by rapid addition of 5 mL of sulphuric acid. The samples were then incubated for 20 min in a water bath at 25°C before measuring absorbance of the supernatant at 485 nm (Perkin Elmer Lambda 2 spectrophotometer, Waltham, Massachusetts). Blank samples were prepared as above but without sediment added. Standard curves were established with glucose solutions ranging in concentration from 10 to 150 mg L^{-1}. Dry weight of the sample was estimated from replicate samples that were dried and weighed.

[15] Chlorophyll *a* served as a proxy for algal biomass. Chlorophyll was extracted with ethanol (90%) for 4 min at 70°C and subsequent sonification for 2 min in an ultrasonic bath set at 40% of the maximum power (Elma Transsonic Digital T790/H, Singen, Germany). The extracts were filtered through two paper filters (MN 619, Macherey-Nagel, Düren, Germany) and absorbance measured at 665 and 750 nm according to standard procedures. No attempt was made to correct for phaeophytin content.

2.4. Physicochemical Parameters

[16] A syringe was used to collect surface and sediment pore water in each sampling period and site of the permanently flowing channels. The water was immediately filtered through prewashed 0.45μm pore size cellulose acetate filters, frozen and later analyzed for nutrients (PO_4^{3-}, NH_4^+, $NO_2^- + NO_3^- = NO_x^-$) according to standard procedures. DOC was measured with a TOC-5000 (Total Organic Carbon Analyzer; Shimadzu, Duisburg, Germany). Influence of freezing on nutrient and DOC concentrations was tested in preliminary trials and found to be negligible at the concentrations measured in the present study. Rainwater collected by a rain sampler in the watershed during each sampling period was analyzed directly after sampling.

[17] To provide information on oxygen availability in the sampled surface sediment, sediment oxygen profiles were measured in situ once in summer 2008 at the six wet and moist sites in each of the three streams. Oxygen profiles were determined with an optode microsensor (0.9 mm diameter; Microx TX3, Presens GmbH, Regensburg, Germany) protected inside a 20 cm long steel tube with a 1.7 mm^2 opening at the tip. The tube was lowered into the sediment to defined depths and pore water was drawn into the tube with a syringe connected to the upper end of the tube. Volumes of 50–100 μL were sufficient to cover the probe tip and avoid mixing of two successive samples. Temperature profiles needed to correct the oxygen data were measured immediately after each oxygen profile by inserting an electronic

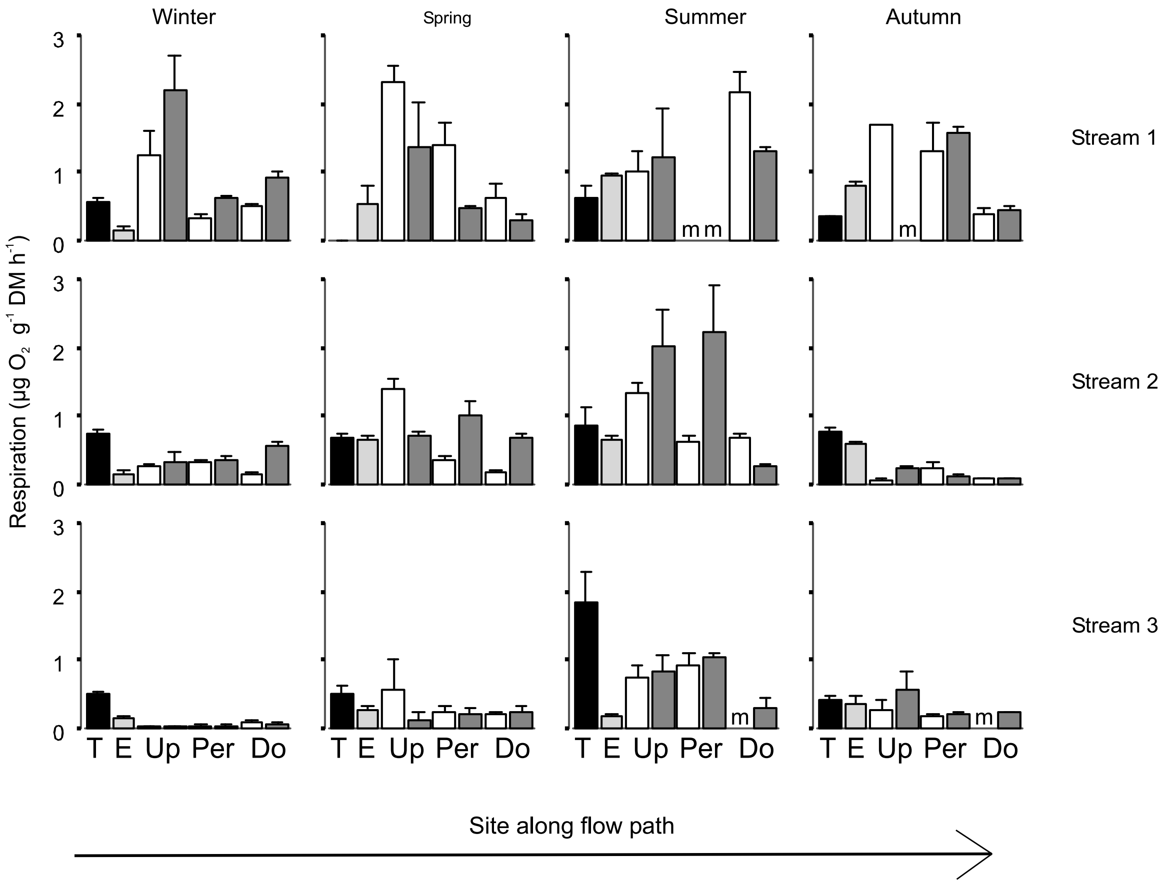

Figure 2. Pattern of respiration rates (means ± 1SE, n = 3) across four seasons at a total of 8 sampling sites along the hydrologic flow path in each of three stream corridors. T, terrestrial (black bars); ephemeral (light gray bars); Up, upwelling; Per, perched surface flow; and Do, downwelling sites. White bars refer to permanently submerged sites within the perennial stream sections and dark gray bars denote parafluvial sites. The m is missing value.

temperature sensor directly in the sediment and taking readings at 1 cm depth intervals.

[18] Sediment grain size distribution was determined by passing combusted soil or sediment (3 analytical replicates per sample) through a series of 11 nested sieves (mesh sizes ranging from 0.032 to 6.3 mm) on a sieve shaker. Total pore volume and water content were determined by drying and weighing an undisturbed core volume (top 2cm, 4 mL).

2.5. Carbon Turnover at the Watershed Scale

[19] To gain insight into the importance of soils and sediments for energy flow integrated at the landscape scale, we calculated carbon turnover at each site and extrapolated the values to a whole year and the entire watershed. As a rough approximation, carbon turnover rates (k) were calculated as the ratio of temperature-corrected community respiration rates (R) to organic matter (OM) standing stocks [*Minshall et al.*, 1983]. Temperature corrections of respiration rates were based on an exponential relationship between temperature and respiratory activity using a Q_{10} value of 2 [*Davidson and Janssens*, 2006]. Respiration rates from seasonal sampling were extrapolated to whole seasons using daily temperature records from the weather station in the watershed. Oxygen consumption rates were converted to carbon units by assuming a respiratory quotient (RQ) of 0.85 [*Hargrave*, 1973], and soil and sediment organic matter (OM) was assumed to contain 40% carbon [*Cahill et al.*, 1987]. Extrapolation to a year (15 November 2007 to 14 November 2008) was based on continuous records of surface runoff in the watershed. Spatial extrapolation was based on GIS data derived from aerial photographs. For soil and sediments of ephemeral channels, respiration on dry days was assumed to be 30-fold lower than respiration measured after rewetting. This approximation is based on the observation that activity has been found in arid environments to increase up to 30-fold after heavy rainfall [*Sponseller*, 2007; *Thomas and Hoon*, 2010]. Results differed little from those of an alternative scenario where respiration at terrestrial sites and ephemeral channel sites was assumed to be nil on days without surface runoff. Microbes at the sites within the perennial stream section were assumed to be permanently active.

2.6. Data Analysis

[20] Results of community respiration were expressed per soil or sediment dry mass (DM), organic matter (ash-free dry mass, AFDM) and surface area based on a soil or sediment depth of 2 cm. Both measured and temperature-corrected respiration rates based on a Q_{10} of 2 [*Davidson and Janssens*, 2006] are presented. Analysis of variance

Table 2. Results of Separate Nested ANOVAs of Respiration, Chlorophyll, and Organic Matter Data From the Chicken Creek Watershed Between November 2007 and 2008

Variable and Source of Variation	df	MS	F	P
Respiration (μg O_2 g^{-1} DM h^{-1})				
Intercept	1	136.6	7.02	0.118
Season	3	13.1	3.31	0.099
Site(stream)	21	1.9	1.84	0.035
Stream	2	19.6	4.06	0.059
Season × stream	6	4.0	3.84	0.003
Season × site (stream)	58	1.1	4.64	<0.001
Respiration at 10°C (μg O_2 g^{-1} DM h^{-1})				
Intercept	1	54.6	12.54	0.071
Season	3	0.5	1.21	0.383
Site(stream)	21	0.5	1.93	0.026
Stream	2	4.4	6.62	0.014
Season × stream	6	0.4	1.57	0.171
Season × site (stream)	58	0.3	4.77	<0.001
Chlorophyll *a* (mg m^{-2})				
Intercept	1	84.3	2.91	0.230
Season	3	6.5	0.96	0.469
Site(stream)	21	1.4	1.38	0.169
Stream	2	29.0	4.06	0.071
Season × stream	6	6.7	6.72	<0.001
Season × site (stream)	59	1.0	4.69	<0.001
Organic matter (mg AFDM g^{-1} DM)				
Intercept	1	234.9	194.13	0.005
Season	3	0.6	4.41	0.058
Site(stream)	21	1.0	7.90	<0.001
Stream	2	1.2	1.21	0.319
Season × stream	6	0.1	1.01	0.428
Season × site(stream)	60	0.1	2.49	<0.001

(ANOVA) was used to test for differences in respiration and other variables among seasons, streams and sites within streams. Season was considered a fixed factor and stream and site nested within stream as random factors. Samples taken in different seasons were considered independent because the study site is highly dynamic and samples were taken several months apart. Since some measurements were missing from different sites in different seasons, use of repeated measures ANOVA would have meant discarding a disproportionately large fraction of the data. When QQ plots, frequency histograms and Wilk-Shapiro's test indicated that residuals did not meet assumptions required for parametric tests, variables (x) were transformed according to $\ln(x + c)$, where $c = \mathrm{q}0.25\ x^2/\mathrm{q}0.75\ x$ and q stands for quantile (Seminar for Statistics, ETH Zurich, personal communication, 2009). Linear regressions were used to explore potential drivers of respiration rates. All analyses were performed with SPSS 15.0. Values in the text are reported as ranges or as means with standard errors.

3. Results

3.1. Metabolic Activity

[21] Metabolic activity in soil and sediments measured as oxygen consumption varied from undetectable to 2.3 μg O_2 g^{-1} DM h^{-1} (Figure 2) and, when expressed per surface area, from undetectable to 3.2 g O_2 m^{-2} d^{-1}. Permanent water availability did not have a major influence on metabolic activity; after rewetting, terrestrial soil and sediments in the ephemeral section had similar respiration rates as sediments in the perennial section. Significant differences were observed along the flow path from soils to the downwelling sites in single seasons and streams. However, there was no consistent temporal pattern (Figure 2). This was reflected in significant interactions of "season × stream" and "season × site nested in stream" in the ANOVA (Table 2). Significance of the "season × stream" interaction disappeared when respiration rates were temperature corrected, but the interaction "season × site within streams" remained significant, indicating that temperature variation was not the only reason for seasonal differences (Table 2).

3.2. Environmental Characteristics

[22] Soil and sediment structure was similar across all sampled sites and seasons, with fine to medium sand as the main fraction ($D_{50} = 201 \pm 4$ μm, $n = 93$). However, silt was about 3–4 times less abundant in sediments (1.3 ± 0.1%) than soil (5.1 ± 0.8%), reflecting preferential downstream transport of the finest particles in the stream channels. Total sediment pore volume did not differ among sampling sites. Water content increased from terrestrial soils (4.9 ± 0.4%, $n = 36$) and the ephemeral channel sites (5.9 ± 0.6%, $n = 36$) to fully saturated in sediments of the perennial sections (15.2 ± 0.1%, $n = 213$).

[23] Surface water concentrations of DOC and nutrients (PO_4^{3-}, NH_4^+, $NO_2^- + NO_3^- = NO_x^-$) varied across streams, seasons and along the flow path but did not show any relation to respiratory activity. PO_4^{3-} and NO_x^- concentrations were low in the permanently flowing stream sections, whereas NH_4^+ and especially DOC concentrations were rather high (Table 1). Pore water concentrations of dissolved nutrients and DOC were in the same range as surface water concentrations. Ammonium concentrations of both pore and surface water generally declined along the flow path in the perennial stream section from 125 to 76 μg L^{-1}, whereas NO_x^- concentrations increased from 15 to 29 μg L^{-1}, suggesting that nitrification occurred in the bed sediments. However, this pattern was not consistent across all streams and seasons. NO_x^- and NH_4^+ concentrations in rainwater, which was used for percolating dry sediments and soil during respiration measurements, were much higher than in stream water, whereas the concentration of PO_4^{3-} was similar and DOC concentrations were lower (Table 1).

[24] Vertical oxygen profiles taken in September 2008 in sediments of the perennial stream sections showed a consistent decline with depth. Oxygen penetrated deeper at the downwelling sites (8 −18 cm) than at the upwelling sites (0.5–6 cm), but there was generally sufficient oxygen at all sites to ensure aerobic microbial metabolism in the upper 2 cm of sediment that were sampled.

[25] Soil organic matter content ranged from 2.1 to 15.1 mg AFDM g^{-1} DM and exceeded the organic matter content of sediments (0.63–5.84 mg AFDM g^{-1} DM) in all seasons (Figure 3). In the perennial stream sections, concentrations of POM that was loosely associated with sediments differed greatly among streams at the time of maximum plant biomass in summer (Figure 4). In contrast, concentrations of POM that was strongly associated with sediments varied little among streams. Loosely associated POM was mainly composed of shoot fragments and seedlings with a minor fraction of amorphous organic matter. Seeds were also present.

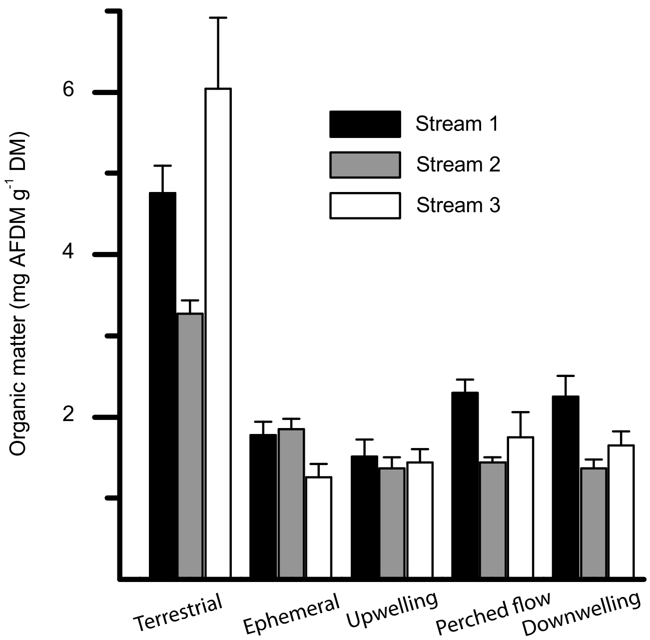

Figure 3. Organic matter content at five sites along the hydrologic flow path in the three mainstreams of the Chicken Creek watershed. Histograms show pooled values over four seasons (mean + 1SE, n = 12). Data from submerged and parafluvial sites in the perennial stream sections were also pooled (n = 24).

[26] Total carbohydrate concentrations in soil and sediments ranged from 0.08 to 3 mg glucose equivalents g^{-1} soil or sediment DM. With one exception, the highest values occurred at the terrestrial sites. Chlorophyll *a* ranged from undetectable to 150 mg m^{-2}, but also varied among stream corridors (Stream 1: 37.0 ± 0.3; Stream 2: 23.8 ± 0.2; Stream 3: 10.2 ± 0.1 mg chl *a* m^{-2}). There was no clear pattern along the flow path or among streams (Table 2). However, parafluvial sediments had higher chlorophyll *a* than submerged sediments (paired *t* test, t = 4.68, p < 0.001, n = 70).

3.3. Organic Carbon Sources for Community Respiration

[27] Regression analysis indicated that respiration rate did not covary with soil and sediment organic matter (R^2 = 0.04, p < 0.001, n = 267) or carbohydrate content (R^2 = 0.09, p < 0.001, n = 198). However, respiration rates in stream sediments showed a positive relationship with chlorophyll *a* content, although this relationship was not very strong (R^2 = 0.42, p < 0.001, n = 233). Adding other environmental factors (e.g., NO_x^-, NH_4^+ or PO_4^{3-} concentration) to a sequential regression model did not increase its explanatory power.

[28] Respiratory activity of sediments from the perennial section measured at one occasion in August 2008 was very similar in sediments percolated with either a mineral nutrient solution or stream water (*t* test, p = 0.83, n = 36). Differences in respiration rates of sediments with and without loosely associated POM suggest that this organic matter fraction supported 58% and 91% of the total respiration per gram sediment DM in streams 1 and 2, respectively, but only 5% in stream 3 (Figure 4a). As concentrations of POM strongly associated with sediment were similar in the 3 streams, this POM fraction could not account for the observed differences in respiratory activity (Figure 4b).

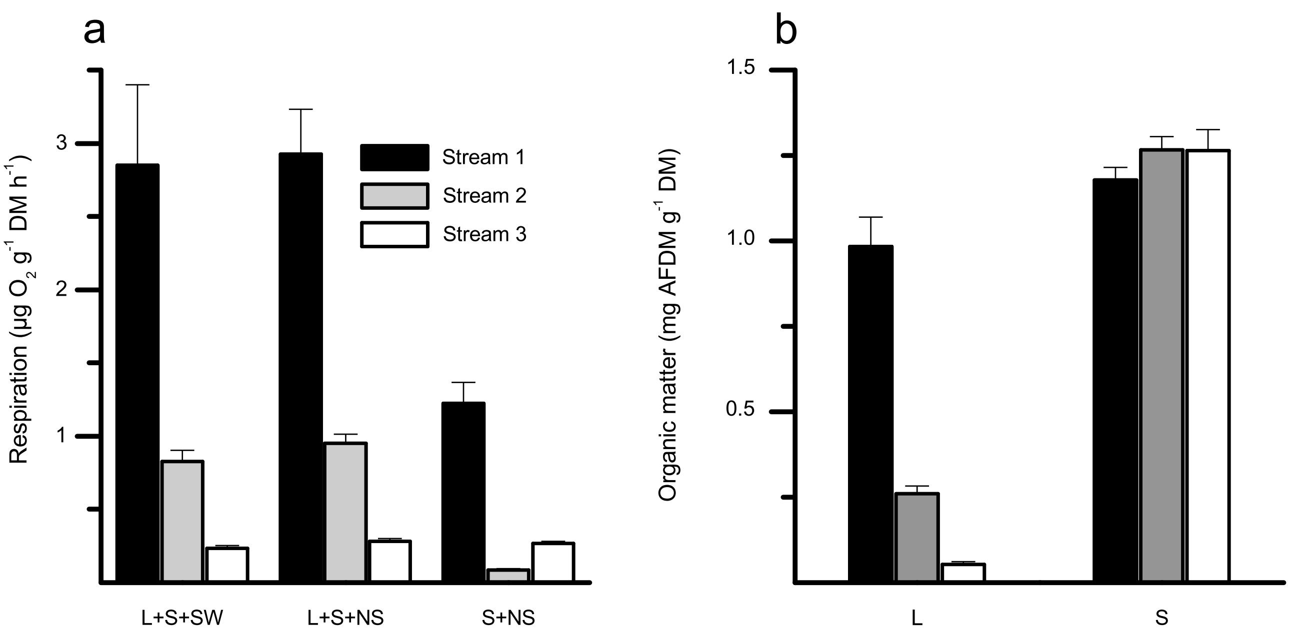

Figure 4. Respiration rates associated with sediment from the perennial sites of the three streams in the Chicken Creek watershed. (a) Respiration rates (means + SE, n = 6) measured in three different conditions to assess the contribution of different carbon sources for sustaining respiration. L, loosely associated POM; S, strongly associated POM; SW, stream water; NS, nutrient solution. (b) Contents of strongly (S) and loosely (L) associated POM in sediments (mean + 1 SE, n = 12).

[29] Carbon turnover rates (k) in the perennial stream sections were fourfold to eightfold higher than at ephemeral and terrestrial sites, ranging from 9.5 ± 1.7 and 12.3 ± 1.8% yr^{-1} at the terrestrial and ephemeral sites, respectively, to 80 ± 23% at perennial sites (n = 3 subwatersheds). When extrapolated to the entire watershed and whole year, the higher rates in the perennial stream sections were insufficient to compensate for the large surface area of terrestrial soils, which accounted for 95% of the total annual carbon turnover in the Chicken Creek watershed. The perennial and ephemeral stream area each accounted for about half of the remaining 5%.

4. Discussion

4.1. Variation of Metabolic Activity Along Flow Paths

[30] A remarkable result of our respiration measurements along the flow path in early successional stream corridors was that potential metabolic activity of rewetted upland soil and sediment from dry stream channels was strikingly similar to rates measured in permanently wet or moist sediments downstream. It appears, therefore, that microbial communities in the young soils and sediments of the Chicken Creek watershed can take rapid advantage of pulses in water availability, raising their metabolism almost instantaneously to full capacity, as has been observed in other circumstances where water availability is low and typically occurs in pulses [e.g., *Cable and Huxman*, 2004; *Kuehn et al.*, 2004]. This observation suggests that permanent water availability is not a main factor determining heterotrophic metabolic potential of microbes in these substrates.

[31] Responses of soil and sediment microbes experiencing mesic climate conditions in the Chicken Creek watershed thus resembles those in semiarid and arid regions, where the short-term stimulating effect of precipitation on microbial activity in soils and ephemeral stream channels is well documented [*Romaní and Sabater*, 1997; *Austin et al.*, 2004; *Belnap et al.*, 2005; *Sponseller*, 2007]. Minor differences in potential microbial activity, measured as Electron Transport System (ETS) activity, were also observed across dry and wet sites in an Australian braided river with sediments mainly composed of shifting sand [*Claret and Boulton*, 2003]. However, full metabolic capacity after rewetting has not been observed in all cases. Often, responses of microbes to sediment rewetting rather appear to depend on the length of the preceding dry period. Rates of both oxygen consumption and ETS activity decreased exponentially for a week as a function of time after sediments fell dry in an ephemeral river in New Zealand [*Larned et al.*, 2007], and bacterial biomass production in a temporary Mediterranean river declined similarly with decreasing water content of sediment submerged for the measurements [*Amalfitano et al.*, 2008]. Thus, full metabolic activity as observed after rewetting of dry soil and sediment in our and other investigations is not a universal phenomenon.

[32] The reasons for the discrepancies among studies are not clear but they might be related to varying degrees of desiccation stress. Differences in soil and sediment structure (e.g., organic matter concentration, grain size) leading to variable protection of enzymes and microbes from desiccation in the mucilaginous matrix of biofilms [*Decho*, 2000] might account for this effect. Different adaptations of microbial communities to drying-rewetting stress frequency [*Fierer et al.*, 2003] and physiological condition of microbes might also have contributed. Consistent with these explanations, microbial biomass production in rewetted stream sediments was more strongly reduced, and recovered more slowly, in a Mediterranean river where desiccation was more severe, and changes in microbial community structure more profound, than in a small temperate stream of Central Europe [*Marxsen et al.*, 2010].

[33] Although potential metabolic activity did not show systematic differences along the flow path in the Chicken Creek watershed, carbon turnover rates were considerably higher in perennial sections of the stream channels. Permanent water availability in the perennial sections facilitated constant microbial activity and, exacerbated by low organic matter contents in the channels, resulted in an overall higher carbon turnover at the aquatic sites. The elevated activity at these metabolic hot spots was insufficient, however, for perennial stream channels to have a strong influence on total carbon flux at the watershed scale. The large spatial extent of terrestrial soils ensured that the annual carbon flux in the whole watershed was still dominated by soil microbial respiration during the hot moments lasting for about 100 days per year when water was available during and shortly after rainfall events.

4.2. Overall Level of Respiration Activity

[34] Sediment respiration per unit surface area in the Chicken Creek watershed was low in comparison to natural sand bed streams (Table 3). This limited activity is not surprising given the scarcity of soil and sediment organic matter in the watershed. It is unlikely to be due to methodological bias because measurements in disturbed soil or sediment samples tend to stimulate rather than curb respiratory activity [*Grimm and Fisher*, 1984]. The low organic matter content (mean of 1.8 with a range of 0.6–5.8 mg AFDM g^{-1} DM) recorded across all sites and seasons is at the low end of values reported even from streams in arid regions (2–12 mg AFDM g^{-1} DM [*Grimm and Fisher*, 1984; *Claret and Boulton*, 2003]) and reflects the initial successional state of the Chicken Creek landscape characterized by sparse vegetation [*Gerwin et al.*, 2009] and limited terrestrial and in-stream primary production. When expressed per soil or sediment organic matter, metabolic activities in the watershed (0–2.9 with a mean of 0.36 mg O_2 g^{-1} AFDM h^{-1}) compare more favorably with respiration rates measured, for example, across a large number of Piedmont streams in the eastern United States (0–0.62 with a mean of 0.41 mg O_2 g^{-1} AFDM h^{-1} [*Hill et al.*, 2002]). However, the rates reported by *Hill et al.* [2002] are also at the low end of published values in streams and have been surmised to be underestimates resulting from respiration measurements in closed centrifuge tubes without advection [*Bott et al.*, 2006]. Thus, low quantity of organic matter is a likely factor limiting respiration in stream sediments and soils of the early successional Chicken Creek watershed.

[35] Low organic matter quality and nutrient limitation are additional potential factors contributing to the low overall respiration activity in the Chicken Creek watershed. In view of relatively low PO_4^{3-} concentrations and high N:P ratios in both stream and rainwater, the most likely limiting nutrient would be phosphorus, which *Mulholland et al.* [2001] found

Table 3. Respiration Rates in Various Streams Comparable to Those of the Chicken Creek Watershed[a]

Stream name	Stream Characteristics and Location	Respiration rate(g O_2 m^{-2} d^{-1})	Reference
Chicken Creek	Sand bed, early successional	0.56 (0.0–3.2)	This study
Fort River	Sand bed, temperate	4.08[b]	*Fisher* [1977]
Sycamore Creek	Sand bed, Sonoran desert	4.1	*Grimm and Fisher* [1984]
Hassayampa Creek	Sand bed, Sonoran desert	(1.33–1.5)	*Uehlinger et al.* [2002]
Rattlesnake Springs	Sand bed, cold desert	7.8[b]	*Cushing and Wolf* [1984]
Creightons Creek	Sand bed, warm temperate, southeast Australia	(0.6–3.7)	*Atkinson et al.* [2008]
Various (N = 64)		16 (2.44–68.1)[b]	*Battin et al.* [2008]

[a]Mean values are reported with ranges in parentheses.
[b]Values converted from g C m^{-2} d^{-1} by assuming a respiratory quotient (RQ) of 0.85 [*Hargrave*, 1973].

to be correlated with whole-stream respiration across a number of different biomes of North America. However, PO_4^{3-} concentrations of stream water and rainwater used to rewet dry sediment and soil from the Chicken Creek watershed showed only minor differences, suggesting that nutrient availability did not account for spatial differences in respiration activity. Furthermore, respiration rates were similar in sediments percolated with either stream water or a mineral nutrient solution. Consequently, it is unlikely that nutrients were a major factor limiting soil and sediment respiration in the Chicken Creek watershed.

4.3. Carbon Sources Fueling Respiration

[36] Several distinct carbon sources were available to fuel metabolism of heterotrophic microorganisms in the stream corridors of the Chicken Creek watershed. These include algal exudates and biomass [*Cole*, 1982], dissolved organic carbon (DOC), and root exudates and litter from the vascular plants that became established in some of the stream channels. Chlorophyll measurements in the Chicken Creek streams (0–150 mg m^{-2} with a mean of 24 mg m^{-2}) indicated that algal biomass was at the low end of values reported from oligotrophic open canopy [*Mulholland et al.*, 2001] and forest streams [*Veraart et al.*, 2008]. However, positive relationships between respiration rate and chlorophyll *a* suggests that at some sites and times algae accounted for a portion of the total community respiration (measurements in the dark), or provided high-quality organic matter that stimulated heterotrophic microbial activity. Similar relationships have been reported from other streams [*Jones et al.*, 1995; *Romaní et al.*, 1998; *Fischer et al.*, 2002].

[37] In the perennial stream sections, a potentially more important carbon source than algae was DOC in upwelling groundwater, which had high concentrations in all streams (Table 1). However, although DOC was abundant, respiration rates of pore water without sediment were exceedingly low, indicating poor bioavailability of this DOC component. This result is consistent with our observation that respiration rates were similar in sediments percolated with DOC-free mineral nutrient solution or DOC-containing stream water (Figure 4a). Furthermore, dark incubation of pore water in bottles inoculated with a microbial cell suspension and shaken daily for 70 days did not lead to a decline in DOC concentration (L. Gerull, unpublished data, 2008). This reinforces our conclusion that DOC in upwelling groundwater in the Chicken Creek watershed was poorly bioavailable and contributed little to overall respiration.

[38] The third important carbon fraction available to heterotrophic microbes in both soils and sediments is particulate organic matter (POM). Similar to other studies [R^2 = 0.15 from *Findlay and Sobczak* [2000] and R^2 = 0.11 from *Uehlinger et al.* [2003]), strong relationships between respiration rate and total POM was not found in the present study, implying that total POM was not a major source of variation in microbial metabolic activity in the Chicken Creek watershed. However, the loosely attached POM fraction, which likely represents small organic particles in sediments [*Pusch and Schwoerbel*, 1994], was strongly related to respiration rate in the perennial stream sections with relatively high plant cover during summer (R^2 = 0.96, $p < 0.001$, n = 18). Loosely associated POM at these sites mainly consisted of dead roots and fragments of herbaceous plants, indicating that, similar to woodland streams [*Fischer et al.*, 1996], POM derived from recent plant production was of prime importance for microbial metabolic activity in the early successional landscape of the Chicken Creek watershed.

4.4. Variation of Metabolic Activity Among Streams

[39] The notable variation in respiration and other response variables (e.g., chlorophyll) that we observed among streams in the Chicken Creek watershed was unexpected. This is because the three studied subwatersheds had formed from the same substrate and were subject to very similar environmental influences during the 2 years of their existence prior to the present study. One explanation for the discrepancies among the streams might be high stochasticity in the early successional landscape that we investigated. Alternatively, the discrepancies could be due to differences in habitat characteristics among the subwatersheds. The most obvious of these was size. Given the flashy surface runoff and discharge regime in the watershed [*Gerwin et al.*, 2009], such size differences could have caused differences in sediment mobility among streams, with the largest stream experiencing the greatest disturbance. Sediment movement during high flow impacts benthic algae [*Cushing and Wolf*, 1984; *Holmes et al.*, 1998; *Atkinson et al.*, 2008]. It also affects macrophyte establishment and persistence [*Riis et al.*, 2004; *Heffernan*, 2008]. This observation is corroborated by a rapid vegetation survey we conducted in the summer of 2008. It showed that vascular plants established more successfully in the smallest than in the largest channel, with the channel of intermediate size (stream 2) in between (L. Gerull, unpublished data, 2008). In contrast to algae and plants, heterotrophic microbial communities appear to show only a minor direct influence of sediment disturbance [*Grimm and Fisher*, 1984]. However, since algae (and vascular plants) can supply significant quantities of dissolved

and particulate organic matter supporting heterotrophic respiration in streams [*Jones et al.*, 1995; *Uehlinger et al.*, 2002], flow-related sediment disturbance could indirectly affect heterotrophic microbial communities as well.

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