A CONCEPTUAL MODEL OF THE FLOW AND DISTRIBUTION OF ORGANIC CARBON IN CAVES

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Abstract: We present a conceptual model for the movement of organic carbon in karst. We argue that the drainage basin is the most appropriate unit for analyzing energy flux in karst. There are two main inputs in karst basins: 1) localized flow of particulate organic carbon (POC) and dissolved organic carbon (DOC) through sinks and shafts and 2) diffuse flow of POC and DOC from soils and epikarst. After entry, this organic matter is processed and transported before eventual loss through respiration or export from the basin. To begin parameterizing our conceptual model, we estimated carbon fluxes for the first two inputs for two karst basins (Organ Cave in West Virginia and Postojna-Planina Cave System (PPCS) in Slovenia) that have sinking streams and many active epikarst drips. We made a series of measurements of organic carbon, especially DOC in epikarst drip water, cave streams, surface streams sinking into the cave, and at resurgences, which we combined with other published data. In both caves, most of the organic carbon entering through the epikarst was DOC, at concentrations averaging around 1 mg C L^{-1}. In both basins, sinking streams accounted for the large majority of DOC input. It is likely that considerable processing of organic carbon occurs within both caves, but more detailed measurements of organic carbon flux at both the basin and stream scale are needed.

INTRODUCTION

It has long been recognized that caves and other subterranean habitats are likely to be food-limited because of the absence of photosynthesis. There is a great deal of indirect evidence such as reduced metabolic rate, larger but fewer eggs, and increased longevity of subterranean animals (see Hűppop, 2000 for a review) that is consistent with the hypothesis of resource limitation. However, there has been remarkably little direct measurement of the input to, and subsequent use of, energy in caves. Indeed, with the exception of a study by Simon and Benfield (2002) in Organ Cave, West Virginia, no one has experimentally tested whether cave streams are carbon or nutrient (nitrogen or phosphorus) limited. In fact, some authors, dating back to Racovitza (1907), have questioned whether caves are food-limited at all.

The lack of emphasis by speleobiologists on the flux of food, especially organic carbon, is all the more remarkable because the discipline of ecology was revolutionized in the 1950s and 1960s by the introduction of ecosystem concepts. Perhaps the most important advance of ecosystem ecology was re-parameterization. Instead of a focus on numbers of individuals, numbers of species, and the like, systems ecology focused on standing stocks and fluxes of matter and energy (especially carbon, phosphorus, nitrogen). Ecosystem ecologists also changed the scale of measurement in ecology. At least in the early days of ecosystems ecology, the spatial scale of analysis tended to be larger than that employed by most population biologists, and took into account multiple features of landscapes such as uplands, riparian areas and streams. For example, the idea of a watershed as a unit of study (Bormann and Likens, 1967), for which input/output budgets could be developed, particularly revolutionized ecosystem ecology. It is ironic that given the nearly complete absence of ecosystem thinking from speleobiology (but see below) that the classic study of energy flux in an ecosystem was that of a karst spring in Florida—Silver Spring (Odum, 1957).

There have been two significant steps forward in ecosystem thinking about cave environments. Historically, the first was the extensive work of Rouch and his colleagues on the Baget Basin, a small karst drainage in France. In a series of more than 20 papers (summarized in Rouch, 1986) he used the ecosystem approach of measuring inputs and outputs of the Baget Basin, but rather than use ecosystem parameters such as carbon and calories, he used numbers of animals. Thus, he used elements of both ecosystem and population ecology. He also made an important conceptual advance of using an entire drainage basin rather than only the cave (Rouch, 1977) as an appropriate unit of analysis in karst. Gibert (1986), in what is the first true ecosystem study in karst, used Rouch's framework and quantified the flux of organic carbon from springs draining the epikarst and the saturated zones of the Dorvan-Cleyzieu basin in France. Among Gibert's most important findings were that dissolved organic carbon (DOC) represented a larger flux than particulate organic

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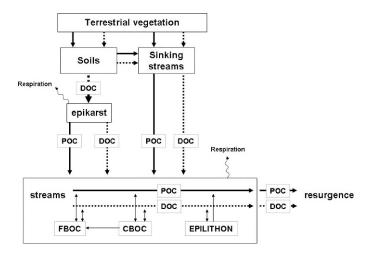
Figure 1. A conceptual model of energy flow and distribution (as organic carbon) in a karst basin. Standing stocks are particulate (POC) and dissolved (DOC) organic carbon in the water column and fine (FBOC) and coarse (CBOC) benthic organic carbon and microbial films on rocks (epilithon). Solid and dashed arrows represent fluxes. Within the cave stream double headed arrows connecting DOC to BOC and epilithon represent leaching and microbial uptake. Double headed arrows connecting POC and BOC represent deposition and suspension. The arrow connecting CBOC and FBOC represents breakdown.
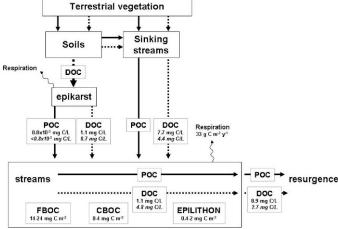

Figure 2. Schematic diagram of organic carbon flux in Organ Cave and the Postojna Planina Cave System (PPCS). Values in italics are PPCS data. Data are standing stocks of C except for respiration flux. POC, DOC, FBOC and CBOC are particulate, dissolved, fine benthic, and coarse benthic organic carbon, respectively. Values for FBOC, CBOC and microbial film are taken from Simon et al. (2003). Whole-stream respiration rate is from Simon and Benfield (2002).

carbon (POC), that those fluxes were temporally variable, and that microbes were likely to be key players in mediating energy transfer between organic carbon and animals in karst. Second, Simon and colleagues applied the methods and paradigms of surface stream ecology to the study of organic carbon cave streams. Among their findings were that most coarse particulate organic matter (CPOM) moved relatively short distances (tens of meters) before it was broken down or consumed (Simon and Benfield, 2001), that cave streams were more likely carbon rather than nutrient limited (Simon and Benfield, 2002), and that microbial films fueled by DOC are an important food in cave streams (Simon et al., 2003).

Our goals in this paper are to: 1) elaborate a conceptual model of energy flow through karst; 2) begin to parameterize this model with existing data from the literature and new data collected from European and North American karst systems; and 3) use these data to compare the various inputs of energy in karst systems and the processing of that energy as it moves through karst.

A CONCEPTUAL MODEL OF ENERGY FLUX IN KARST

The most appropriate scale for an ecosystem approach to studying energy flow in karst is one that includes the relevant energy sources to caves and one for which input-output budgeting may be used. The karst basin used by

Rouch satisfies both requirements. Energy inputs to karst basins can include internal production and the import of DOC and POC derived ultimately from surface vegetation. While some karst basins may have substantial internal energy production by chemoautotrophs (e.g., Sarbu et al., 1996), in most karst basins, internal production is effectively zero. Input of DOC and POC may arrive via two different pathways (Fig. 1). Localized openings such as sinking streams and shafts permit entry of DOC or POC, such as leaves, wood, and fine detritus from streams and soils. Water percolating through soils and the epikarst, the zone of contact between soils and bedrock lying above caves, carries with it DOC, but POC is effectively filtered by soils (Gibert, 1986). POC may arrive from the epikarst in the form of animals dripping into caves through the epikarst. While localized input of organic carbon is the most easily observed and likely to be large, there is considerable reason to think that diffuse input from the epikarst is also important. For example, Pipan (2005) has shown that there is a rain of POC in the form of copepods in epikarst drips, and Simon et al. (2003) found that microbial films fueled by DOC from soils were a primary food for animals in cave streams.

For terrestrial habitats in caves there is another source of carbon, movement of organic matter into the cave through entrances, especially from animals that regularly enter and exit the cave (e.g., bats and crickets). In some circumstances, bat guano may enter the cave stream (Graening and Brown, 2003), and we consider this part

of the localized transfer of organic carbon. Deep ground water may be another source of DOC, but considering the long residence time and distance from organic matter sources, deep ground-water inputs likely contribute little organic carbon within karst basins.

After input into the karst basin, POC and DOC are used or processed to different forms before eventually being exported through resurgences (Fig. 1). The major standing stocks of organic carbon within the basin include DOC and POC (or, seston) in the epikarst, epikarst drips, sinking streams, and cave streams, and POC (either fine (FPOC), <1 mm, or coarse (CPOC) >1 mm) and microbial films on rocks (epilithon) in epikarst and cave streams. The major fluxes of organic carbon include transport of DOC and POC in drips and streams (sinking and within caves), suspension and deposition of CPOC and FPOC in streams, breakdown of CPOC to FPOC, leaching of DOC from POC and epilithon, uptake of DOC by epilithon and microbes associated with benthic POC, losses from respiration along the flowpath of water through the basin, and export from springs (Fig. 1). While ideally the standing stocks and fluxes within the epikarst should be included within the karst basin, operationally this is virtually impossible given the inaccessibility of the epikarst. Therefore, only the fluxes out of the epikarst are likely to be directly measurable.

Within karst basins, standing stocks and fluxes of organic carbon are likely to be both spatially and temporally variable. This variation is likely to be important, but given the paucity of data, our focus is primarily on the conceptual model and includes only an initial parameterization of standing stocks and fluxes of energy. In particular, we do not address temporal variation in standing stocks or fluxes of carbon and only touch upon spatial variation among epikarst drips. These issues we leave for future, detailed analysis.

Methods and Materials

We parameterized models of two cave systems: Organ Cave in West Virginia and Postojna-Planina Cave System (PPCS) in Slovenia. We used published estimates for some standing stocks and fluxes for Organ Cave (Simon and Benfield, 2002; Simon et al., 2003). We also collected new data about inputs of organic carbon through epikarst drips and sinking streams, as well as DOC in cave streams and the resurgences, of both systems.

Organ Cave is a large, mostly horizontal cave with over 60 km of surveyed passage located in Greenbrier County, West Virginia (Stevens, 1988). Organ Cave drains an 8.2 km^2 basin, 70 percent of which is underlain by Mississippian limestone and the rest by Mississippian sandstone and shale. A series of small cave streams eventually coalesce in a single stream that emerges at a spring on the edge of Second Creek, itself a tributary of the

Greenbrier River, the base stream of the region. Small streams, some of them seasonal, that originate in a non-carbonate part of the basin, sink at or near some of the nine entrances to the cave system. Most of the land in the basin is agricultural, especially pastures. Organic carbon samples were taken at one stream that sinks into the cave near the Organ Cave main (commercial) entrance, three small streams in the cave, Lipps, Sively No. 2, and Sively No. 3 (all place names can be found in Stevens (1988)), 13 epikarst drips (see Pipan and Culver [2005] for locations) draining into the three streams, and the resurgence of the system.

The Postojna-Planina Cave System (PPCS), with approximately 23 km of surveyed passage (17 in Postojna and six in Planina connected by 2 km of flooded passage), is arguably the most extensively studied cave in the world (e.g., Pipan and Brancelj, 2004; Sket, 2004). There are two main streams in PPCS which join and exit at Planina Cave entrance. One stream is formed by the Pivka River, a moderate-sized river draining approximately 230 km^2 of carbonate and flysch which sinks near the Postojna Cave entrance. The other stream (Rak) is a somewhat smaller stream draining approximately 27 km^2 of carbonate and flysch. The land over PPCS, which is developed in Upper Cretaceous carbonate rocks, is forested, and the Pivka River drains land with a variety of uses, including forest and agriculture, as well as several small towns. The area over the cave system itself is approximately 20 km^2. Samples were taken at 28 drips in Postojna Cave (see Pipan (2005) for locations), five drips in Planina Cave (Pipan, unpublished), the two cave streams, the Pivka River where it enters the cave, and one resurgence, the Unica River.

An important difference between the two sites is the extent to which the cave fills the drainage. The ratio of cave passage length to basin size is 7.3 km^{-1} in the Organ Cave basin and 0.089 km^{-1} for the PPCS basin. The difference is largely the result of differences in drainage area and cave morphology (Palmer, 1991).

For the epikarst estimates, we collected water samples from epikarst drips and cave streams between April 2006 and November 2006. For drips, water was collected in acid-washed 50 mL HDPE sample bottles over the course of at most one hour, depending on drip rate, which ranged between 75 and 1500 mL h^{-1}. This minimizes losses of DOC in the sample (see Emblanch et al., 2005). Water was then placed in a 60cc syringe and passed through a 0.45 μm glass fiber filter (Gelman GF/F) into a second bottle and preserved to pH < 2 with a drop of concentrated HCl. Water from streams was collected directly in a syringe and then filtered and preserved as above. The samples were analyzed for DOC concentration using the persulfate digestion method (APHA 1999) on an OI Analytical Total Organic Carbon Analyzer Model 1010.

We estimated the standing stock of POC, as copepods and other organisms, from the portions of the epikarst to cave streams by using data on numbers of individuals caught in 60 μm nets given in Pipan (2005) and Pipan et al.

Table 1. Estimates of dissolved organic carbon from Organ Cave and PPCS.

Cave Inflows	Organ Cave			Postojna-Planina Cave System		
	n	Mean, mg C L^{-1}	S.E.	n	Mean, mg C L^{-1}	S.E.
Sinking streams	3	7.67	1.03	2	4.36	0.46
Epikarst drips	20	1.10	0.15	99	0.70	0.04
Cave streams	6	1.08	0.32	3	4.75	1.57
Resurgence	3	0.90	0.17	2	2.67	0.80

(2006). We converted the numbers of animals entering to organic carbon by measuring the ash-free dry mass of 100 copepods obtained from Carolina Biological Supply.

RESULTS

For Organ Cave, DOC concentration in sinking streams was seven times higher (7.67 mg C L^{-1}) than in epikarst drips (1.10 mg L^{-1}, Table 1), a statistically significant difference (t = 6.32, df = 2, p < 0.02). Individual drips showed considerable variation (CV = 0.62), but we do not yet have enough spatial or temporal data to make any statements about pattern. On average, epikarst drips and the cave streams had similar concentrations of DOC (Table 1, t = 0.039, df = 7, p = 0.48). Interestingly, the concentration of DOC was lower in the Lipps stream (0.73 mg L^{-1}) which is entirely epikarst fed (Simon and Benfield, 2001), than in the other streams (1.25 mg L^{-1}), but the difference was not statistically significant. In a paired sample taken in May 2006, the DOC concentration in Lipps stream, which was fed by epikarst water, was five times lower (0.19 mg L^{-1}) than in a drip feeding it (1.01 mg L^{-1}). In August 2006, the concentration of DOC in Lipps streams (1.26 mg L^{-1}) was about 75 percent that of two drips (1.72 mg L^{-1} and 2.48 mg L^{-1}) that fed the stream. If our drip samples were representative of all the epikarst water feeding the stream, then it appears that there is considerable processing of DOC along the epikarst-stream flowpath. DOC concentration in the resurgence of Organ Cave was similar to that in the epikarst drips and cave streams (Table 1).

In PPCS, DOC concentration in the sinking streams was also higher (4 times) than that in the epikarst drips (Table 1, t = 7.87, df = 1, p = 0.04). The DOC concentration in sinking streams of PPCS was 43 percent lower than that at Organ Cave (t = 2.93, df = 2, p = 0.03). For epikarst drips in PPCS, DOC concentration was slightly (t = 2.57, df = 21, p < 0.01) lower than in Organ Cave and the variation among drips was slightly less in PPCS (CV = 0.53). Unlike in Organ Cave, DOC concentration in the cave streams of PPCS was high and similar to that in the sinking streams (Table 1). At the resurgence of PPCS, DOC concentration was intermediate between the streams and epikarst drips. Compared to the resurgence of Organ Cave, the resurgence of PPCS had significantly higher DOC (t = 6.32, df = 2, p = 0.02).

Finally, we estimated the standing stock of POC, as copepods, in epikarst drips. The average ash-free dry mass (AFDM) of a copepod, 1.6×10^{-3} mg per individual, was converted to carbon (0.72×10^{-3} mg C per individual) assuming AFDM was 45 percent C (Sinsabaugh, 1997). In Organ Cave, Pipan et al. (2006) estimated copepod density to be 0.0041 copepods/L, equating to 2.95×10^{-6} mg POC L^{-1} in epikarst drips. This value is about 6 orders of magnitude lower than the average standing stock, 1.10 mg DOC L^{-1} in epikarst drips (Table 1).

DISCUSSION

From an ecosystem perspective, cave streams are very similar to a rather unproductive surface stream (Simon and Benfield, 2001, 2002). Indeed, the concentration of DOC in streams of Organ Cave and PPCS are at the low end of the range (0.1 to 36.6 mg L^{-1}) reported for surface streams (Muholland, 1997). The standing stocks of particulate organic matter in Organ Cave streams are also quite low (Simon and Benfield, 2002). It is important to note that most data available for examining energy distribution in karst are standing stocks, not fluxes (Fig. 2). We know of only three estimates of energy flux in karst systems. Gibert (1986) quantified the annual flux of organic carbon from springs draining portions of the Dorvan-Cleyzieu basin; Graening and Brown (2003) estimated flux of organic matter into and out of a reach of a cave stream; and Simon and Benfield (2002) measured whole-stream respiration in a stream in Organ Cave. This places considerable restrictions on our ability to generalize, but we can use the data we have to speculate on how karst systems process energy and what further data are needed.

At both the aquifer (Gibert, 1986) and stream reach (Graening and Brown, 2003) scales, DOC is the largest input of organic carbon in karst. The concentration of DOC was much higher in sinking streams than in epikarst in both basins we examined. The relative importance of those two sources in a karst basin depends, in part, on the magnitude of those flows (i.e. the concentration times the volume of water entering from each source). We do not know the total amount of water entering the basins through epikarst drips and sinking streams, but we can use drainage area as a surrogate. It is difficult, if not impossible, to estimate the average drainage area of a drip, especially since water entering from the surface is stored in

the epikarst (Williams, 1983) and some, perhaps even most, of the water stored in epikarst enters the water table without ever being intercepted by a cave passage. Nevertheless, if we conservatively assume that all the epikarst water ultimately arrives in cave streams, we can use the proportions of the basins draining to sinking streams and assume the remainder drains through the epikarst. In the Organ Cave basin, sinking streams drain 30 percent of the basin at a DOC concentration of 7.67 mg L^{-1} (Table 1), while the epikarst drains 70 percent of the basin with a DOC concentration of 1.10 mg L^{-1} (Table 1). Even if all this epikarst water ends up in the cave, which seems highly unlikely, the expected contribution of DOC from sinking streams is about three times higher than that supplied by the epikarst. The figures for PPCS are even more striking. Sinking streams drain a much larger proportion of the basin (93%) and, when combined with DOC concentrations, sinking streams account for 99 percent of the DOC entering the subsurface.

However, the relative amount of DOC entering from epikarst and sinking streams will not be the sole determinant of the importance of those two carbon sources. First, DOC is a complex mix of organic molecules that differ in quality as energy sources and DOC composition likely differs between epikarst and sinking streams considering their differing origins. Second, the spatial distribution of percolating water is more widespread than that arriving in streams. Not all caves have sinking streams and many streams and pools in caves can be fed exclusively by percolating water. In these circumstances, the only source of organic carbon to much of the aquatic habitat in caves would be percolating water. Of course, there may also be cave passages deep underground with few or no drips, and it is likely that DOC decreases with depth, as it does in alluvial aquifers (Pabich et al., 2001, Datry et al., 2005). Third, the residence time of water arriving through epikarst drips and sinking streams is likely to be quite different. Most drip-fed streams are small, allowing greater time for organic matter uptake and processing than in fast-flowing, large channels fed by sinking streams. Ultimately, the relative importance of epikarst and sinking streams as organic carbon sources will depend on the relative magnitude of carbon flux arriving from each flow path, the composition of organic carbon arriving from each source, the residence time of water arriving via each flowpath, and the spatial extent of habitat fed by each source. These factors will need to be integrated into models of energy flux in karst and they may be quite variable among karst systems depending on the geological structure of the basins and distribution and composition of vegetation and soils on the surface.

How much biological processing of organic matter entering karst occurs is unclear. Processing of POC at the stream reach scale can be quite efficient in caves. For example, in Organ Cave most coarse organic matter (leaves and sticks) is transported only a few hundred meters into the cave before it is retained and broken down into smaller particles or consumed by animals and microbes (Simon and Benfield, 2001). In addition, rates of organic carbon turnover, estimated from organic carbon standing stocks and rates of metabolism, in Organ Cave streams are high compared to surface streams (Simon and Benfield, 2002). Processing of organic carbon at the basin scale is unknown. On one hand, in both Organ Cave and PPCS, DOC concentration at the resurgences was lower than that arriving through surface streams and in the streams within the caves, suggesting DOC was consumed in the aquifer. On the other hand, DOC concentration in the epikarst drips was similar to or lower than that at the resurgence, a trend also found in the Dorvan-Cleyzieu basin (Gibert, 1986; Simon et al., 2001). This highlights the need for careful measures of carbon flux, rather than only standing stocks, into and out of karst basins to generate mass balances that can be used to measure organic carbon processing at the basin scale. This may be difficult considering it may not be possible to access all portions of a basin. For example, Gibert (1986) measured the annual fluxes of DOC and POC from a spring draining a portion of the epikarst and another spring draining the base of the Dorvan-Cleyzieu basin, but these springs represented only a portion of the water moving through the basin, making it impossible to calculate whole-basin processing of organic carbon. Linking data regarding carbon fluxes in portions of basins to hydrological models of the whole basin may provide a means of scaling up carbon studies to the whole-basin level.

Conclusions

We believe an ecosystem perspective applied to karst holds the potential to greatly increase our understanding of the ecology and evolution of karst systems. The greatest challenges, and most promising data, will arrive from a careful accounting of inputs and outputs to a karst basin and measures of standing stocks and fluxes (transport and respiration) within basins. Ultimately, this will need to include an analysis of the quality and spatial and temporal distribution of organic matter inputs and outputs in karst. In comparing Organ Cave and PPCS, some similarities (e.g., lower DOC concentration in epikarst than sinking streams) emerged, but there were also differences (e.g., concentration of DOC in cave streams relative to other locations in the basin). This suggests that there will be some common features of organic carbon flux in karst, but not all basins will function the same. A careful integration of basin structure and hydrology should enhance our understanding of how different basins function.

Acknowledgements

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