

# Influences of travertine dam formation on leaf litter decomposition and algal accrual

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Received: 12 January 2006 / Revised: 28 July 2006 / Accepted: 2 August 2006 / Published online: 29 September 2006  
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**Abstract** At the time of this study Fossil Creek was being considered as a site for the restoration of a native fish assemblage, however there was concern amongst fisheries managers about the stream being food limited due to calcium carbonate (travertine) deposition. To evaluate the effects of travertine deposition on the aquatic food base we used leaf litterbags to compare decomposition rates and nutrient diffusing artificial substrates to compare algal accrual rates and nutrient limitation between two distinct reaches in Fossil creek: a travertine dam forming reach and a reach without travertine dam formation (riffle-pool reach). Decomposition was significantly faster in the travertine dam forming reach

than in the riffle-pool reach. Macroinvertebrates in the leaf packs were more diverse in the travertine reach but more abundant in the riffle-pool reach. Algae accrued more quickly in the travertine reach than in the riffle-pool reach and only responded to nutrient enrichment in the travertine reach. This study was conducted prior to a hydroelectric dam decommissioning project in Fossil Creek where full flows were reintroduced back into the stream after a century of diversion. Our results suggest concurrent increases in algal productivity, decomposition, and macroinvertebrate diversity in the next decade as travertine dams rebuild, providing a richer food base for fish and other aquatic organisms.

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Handling editor: K. Martens

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**Electronic Supplementary Material** Supplementary material is available to authorised users in the online version of this article at <http://dx.doi.org/10.1007/s10750-006-0379-6>

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**Keywords** Travertine · Geomorphology · Leaf litter decomposition · Algae · Algal accrual · Nutrient limitation · Phosphorous · Nitrogen · Invertebrate · Dam · Hydroelectric · Native fish · Food base

## Introduction

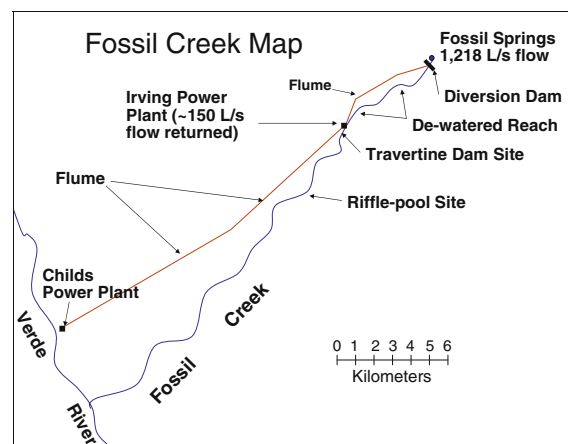
On land and in fresh waters, geological processes strongly shape ecosystems (Dokuchaev, 1883; Jenny, 1941; Vannote et al., 1980; Minshall et al., 1983). In rivers, geomorphology can influence biota and nutrient cycling (D'Angelo et al., 1993; Valett et al., 1996; Doyle et al., 2003). Travertine

streams are compelling systems to study the interplay between geomorphology and biology because of the potential for reciprocal interactions. Travertine forms in waters high in calcium carbonate as  $\text{CO}_2$  degasses causing calcium carbonate to precipitate out of the water and deposit in the stream channel (Barnes, 1965; Stumm & Morgan, 1970). Biotic processes influence the rate of travertine deposition, sometimes changing stream morphology through the construction of travertine dams (reviewed in Pentecost, 2003).

The connections between biotic processes and travertine formation have been studied in many ecosystems (reviewed in Pentecost, 2003). Eucaryotic algae and cyanobacteria, commonly associated with travertine formations worldwide reduce  $\text{CO}_2$  concentrations through photosynthesis, facilitating the precipitation of calcium carbonate in many ecosystems (marine, Golubic et al., 2000; caves, Cacchio et al., 2003; aquifers, Warren et al., 2001; thermal pools, Zhang et al., 2004; lakes, Freydet & Verrecchia, 1998; and streams, Emeis et al., 1987). Fewer studies have addressed how travertine affects ecological processes. This study focuses on the influence of travertine dam deposition and geomorphology on two of the most important inputs of energy into the food base of stream ecosystems: allochthonous energy in the form of terrestrial leaf litter, and autochthonous energy in the form of algal accrual (Allan, 1995). The quantity and assimilation of these two forms of energy depend upon broad-based ecosystem processes (Webster & Benfield, 1986; Marks et al., 2000), which may be affected by travertine dam formation. Leaf litter decomposition is ecologically important because the processes of nutrient leaching, fungal and bacterial colonization, feeding and shredding by macroinvertebrates, and mechanical fragmentation of the leaf material makes the energy in the leaves available to a wide variety of aquatic organisms throughout different trophic levels (Benfield, 1996). Leaf litter decomposition may be retarded by travertine especially if calcite precipitates on the leaf litter surface (Casas & Gessner, 1999; LeRoy & Marks, 2006). Travertine deposition has also been implicated in reducing aquatic macroinvertebrate biomass and diversity (Oberlin et al., 1999).

This experiment was conducted prior to a hydroelectric dam decommissioning project in Fossil Creek where approximately 90% of flow was reintroduced back into the stream after a century of diversion. Historical accounts of Fossil Creek describe a series of travertine terraces and pools with the highest terraces reaching three m (Chamberlain, 1904). From 1909–2005 the majority of base flow ( $\sim 1,200 \text{ l s}^{-1}$ ) was diverted outside the stream channel for hydropower production, significantly reducing discharge, travertine precipitation, and travertine dam formation (Fig. 1). Geomorphologists predict that within a decade after return of full flows travertine dam formation will increase substantially (Overby & Neary, 1996; Malusa et al., 2003; Marks et al., 2006).

At the time of this study Fossil Creek was under consideration to be managed exclusively for native fishes. The native fish fauna in the southwestern United States has declined alarmingly since Euro-American settlement (Minckley & Deacon, 1991; Rinne & Minckley, 1991). Many species are listed as threatened or endangered (USFWS, 2005). Efforts at conservation can be costly (USFWS, 2003); therefore, candidate recovery streams should be chosen wisely. Managers were concerned that increases in travertine deposition in Fossil Creek would substantially reduce food availability for fishes (FERC, 1997). This research tested for differences in the food base between two reaches with dramatically different morphologies but the same



**Fig. 1** Map of Fossil Creek including the hydroelectric plants, the water transport flume, and the relative positions of the study sites

water source, flow rate, and climate, to thereby infer how the food base would change with increased travertine deposition. The travertine dam forming reach, with steep cascades and deep pools, was indicative of the dominant morphology expected after restoration whereas the riffle-pool morphology (without travertine dams) dominated the morphology of the stream over the last century. Previous studies in travertine systems suggest that increased travertine could retard leaf litter decomposition due to calcite encrustation (Casas et al., 1994; Casas & Gessner, 1999) decreasing the abundance and diversity of associated macroinvertebrates. Although some macroinvertebrates are associated with travertine (Drysdale, 1999; Dinger, 2001) we expected that many macroinvertebrates would be inhibited by travertine, explaining the low diversity described in another travertine stream (Oberlin et al., 1999). We expected to observe strong phosphorus limitation of algae in the travertine reach because of the propensity for phosphorus to bind with calcium (Wetzel, 2001). Associations of nitrogen fixing cyanobacteria with travertine (Golubic, 1973; Frey et al. & Verrecchia, 1998; Pentecost, 2003), argues against strong nitrogen limitation in travertine areas. In contrast, we expected strong nitrogen limitation in the riffle-pool reach as has been observed in other Arizona streams (Grimm & Fisher, 1986). Specifically, this study addressed the following three questions: (1) Does travertine dam formation retard leaf litter decomposition, and reduce the abundance and diversity of macroinvertebrates found in leaf litter? (2) Is travertine dam formation associated with high or low levels of algal accrual and diversity? (3) Are algae more nutrient limited in a travertine dam forming reach than a riffle-pool reach?

## Materials and methods

### Study sites

Fossil Creek is located on the Mogollon rim in central Arizona (Fig. 1). It is fed from perennial springs at an elevation of 1690 m. The springs flow at a nearly constant volume of  $1,218 \text{ l s}^{-1}$  (Malusa et al., 2003). The spring water is warm

year round, coming out of the ground at  $19\text{--}23^\circ\text{C}$  (Neve, 1976). The travertine reach used in this study occurred immediately below the first power plant, (Fig. 1). During this study the hydropower facility was operating and active travertine dam formation was concentrated below the Irving Power Plant where some diverted water ( $\sim 150 \text{ l s}^{-1}$ ) was returned to the stream channel forming a short reach ( $< 1 \text{ km}$ ) with numerous travertine dams, giving the channel a terraced, step-pool morphology. These dams were approximately 1–2 m high and formed pools that ranged from just a few square meters to over 500 square meters in surface area. Pool depths averaged 1–2 m and the stream widths averaged approx 8–14 m. Travertine dams began to dwindle approximately 1 km downstream from the Irving power plant as calcium carbonate concentrations decreased. Approximately 3 km downstream from the Irving power plant no travertine dams were observed. The active travertine forming reach was in stark contrast with the lower portion of the stream, which had a riffle-pool morphology. Widely scattered deep pools existed but most of the reach was made up of shallow riffle-runs.

The travertine reach had consistently higher concentrations of nitrate and phosphate but did not differ in the other nutrients measured (Table 1). Atomic ratios of N:P were similar between the two reaches (near 11), so travertine does not appear to alter the stoichiometry of these elements. Calcium concentrations decrease downstream as travertine deposition removes calcium from the water column. Water temperature during the winter was higher at the travertine reach than at the riffle-pool reach, while temperatures during the summer were nearly equal (Table 1). The water from the warm springs traveled rapidly down the diversion flume, with little time to lose heat before arriving at the Irving power plant and the travertine reach (Fig. 1). In the winter heat loss was rapid in the main channel accounting for differences between the sites. In contrast heat loss was minimal in the summer.

### Leaf litter decomposition

Leaf litter from two species of trees, Arizona alder *Alnus oblongifolia* Torr., and Arizona syc-

**Table 1** Water quality data collected at collected at the travertine dam reach (Trav.) and the riffle-pool reach during three seasons from August 2002 to May 2003

	8/15/2002		12/5/2002		5/6/2003	
	Trav.	Riffle-pool	Trav.	Riffle-pool	Trav.	Riffle-pool
Temp (°C)	23.04 (0.05)	22.8 (0.02)	20.04 (0.7)	12.5 (0.01)	20.3 (0.06)	19.2 (0.02)
PH	7.8 (0.04)	8.33 (0.01)	7.81 (0.03)	8.23 (0.04)	8.15 (0.01)	8.5 (0.01)
DO (mg l <sup>-1</sup> )	7.39 (0.06)	7.4 (0.05)	8.1 (0.02)	9.43 (0.03)	6.98 (0.07)	7.95 (0.13)
DO% (% Sat)	111 (0.9)	110 (0.65)	114 (0.5)	113 (0.4)	100 (0.81)	111 (1.95)
Cond. (μS cm <sup>-1</sup> )	749 (1.7)	514 (0.3)	730 (0.5)	564 (0.2)	679 (0.2)	501 (0.2)
PO <sub>4</sub> (mg l <sup>-1</sup> )	0.047 (0.01)	< 0.04	0.043 (0.005)	< 0.02	0.1 (0.04)	< 0.02
NO <sub>3</sub> (mg l <sup>-1</sup> )	0.09 (0.01)	< 0.02	0.46 (0.05)	0.21 (0.06)	0.11 (0.006)	< 0.02
Mg (mg l <sup>-1</sup> )	42 (0.17)	41 (0.2)	35 (0.5)	36 (0.3)	35 (0.52)	35 (0.06)
Ca (mg l <sup>-1</sup> )	100.8 (3.2)	22.7 (1.2)	85 (0.8)	51.2 (0.4)	85.8 (0.26)	46.5 (0.3)
Na (mg l <sup>-1</sup> )	12.2 (0.3)	12.9 (0.12)	10.5 (0.24)	10.7 (0.12)	10.8 (0.15)	11.2 (0.12)
K (mg l <sup>-1</sup> )	2.1 (0.06)	2.2 (0.1)	1.5 (0.12)	1.5 (0.12)	1.6 (0.06)	1.7 (0.1)
Cl (mg l <sup>-1</sup> )	5.7 (0.2)	6.5 (1.07)	9.1 (0.57)	8.5 (0.12)	8.1 (0.25)	8.13 (0.12)
SO <sub>4</sub> (mg l <sup>-1</sup> )	24.4 (0.3)	23.8 (0.05)	24.6 (0.2)	24.4 (0.17)	23.5 (0.2)	24 (0.02)

Mean values are given with standard deviations in parentheses ( $n = 3$ ) Mean values are given with standard deviations in parentheses ( $n = 3$ )

amore *Platanus wrightii* S. Watson, was collected by hanging tarps under trees to catch leaves after natural abscission. We used fast (alder) and slow (sycamore) decomposing species that are common along Fossil Creek (LeRoy & Marks, 2006) to test if the slow decomposer would become more encrusted with travertine because it is in the stream for a longer period of time whereas the fast decomposer may decompose prior to being encrusted.

The leaves were taken to the lab and dried to constant mass. Four grams of leaf litter were placed into 6 mm mesh bags and sewn with monofilament fishing line. On 11/20/2002, leaf litterbags were attached to rebar anchors and placed in the stream in areas where naturally forming leaf packs occurred (pools, eddies, stream margins, and against the upstream side of travertine dams) along a 0.5 km length of the travertine dam reach, and a 1.5 km length of the riffle-pool reach. Additional leaf litterbags were filled, brought to the study site, and then taken back to the lab to be processed for handling loss estimates. These leaf litterbags were used as time zero samples. About 10 leaf litterbags per species, per site, were retrieved from the stream at each harvest period: 7 days, 14 days, 21 days, 28 days, and 56 days (a final harvest date was scheduled for 112 days but all leaf litterbags were destroyed by a late winter flood). Each litterbag was placed

in a zip-lock bag, transported to the lab in a cooler, and processed within 24 h. In the lab, the leaf litter was removed from the bags and gently rinsed of silt and debris. Macroinvertebrates were collected from each sample and stored in 70% ethanol. The leaf litter samples were dried at 70°C until reaching constant mass (24–48 h) and weighed. Samples were combusted at 500°C for 1 h, desiccated for 30 min, and re-weighed to determine ash free dry mass (AFDM). Invertebrates were collected from the leaf litterbags from the 14-day harvest and 28-day harvest. Invertebrates were picked, sorted and identified (mostly to genus) under a dissecting scope using manuals by Merritt & Cummins (1996), Thorpe & Covich (2001), and Wiggins (1996).

Leaf litter decomposition rates were calculated by regressing the ln (AFDM remaining) against incubation days for each treatment. The negative slope of the regression line ( $k$ ) is equal to the decomposition coefficient. Site to site and species to species differences were tested for statistical significance by using an ANCOVA procedure testing for homogeneity of slope. Whole model and 2 by 2 interaction effects were tested using incubation days as a covariate and both site and species as main effects. Differences in leaf litter decomposition rates were also assessed using ANOVA, comparing mean ln (AFDM) at each harvest between sites and leaf species. Shannon-

Wiener diversity scores were calculated for macroinvertebrate taxa. To assess differences in invertebrate community composition at the two reaches, Non-metric Multidimensional Scaling (NMDS) and Multi Response Permutation Procedure (MRPP) analyses were performed using the PCORD statistical package (McCune & Mefford, 1999). MRPP is similar to multivariate analysis of variance without the requirement of multivariate normality and homogeneity of variance (Mielke, 1984; Biondini et al., 1985). It tests the hypothesis of no difference between two or more groups with significance inferred at  $p = 0.05$ . Non-metric multi-dimensional scaling (NMDS) produces a two-dimensional graphical representation or 'map' of the similarity relationships between samples. NMDS is an ordination method based on ranked distances that is suitable for analyzing ecological data that do not meet the assumptions of parametric tests (McCune & Mefford, 1999). Sorensen's coefficient was used as the distance measure for NMDS.

#### Algal accrual and nutrient limitation

This experiment was conducted three times (start dates: 11/6/2002, 1/26/2003, and 5/29/2003) to test for seasonal differences, as well as reach to reach differences, in algal accrual and nutrient limitation. Nutrient diffusing artificial substrates were constructed using 8.9 cm diameter clay flowerpots (Fairchild & Lowe, 1984). Flowerpots were filled with 2% agar and 1 of 4 treatments: (1) Nitrogen enrichment,  $0.5 \text{ mol l}^{-1} \text{ NaNO}_3$ ; (2) Phosphorous enrichment,  $0.1 \text{ mol l}^{-1} \text{ Na}_3\text{PO}_4$ ; (3) Nitrogen + Phosphorous enrichment,  $0.5 \text{ mol l}^{-1} \text{ NaNO}_3 + 0.1 \text{ mol l}^{-1} \text{ Na}_3\text{PO}_4$ ; (4) Control, 2% agar only. Four pots (one pot of each treatment) were attached to a  $0.5 \times 0.5 \text{ m}$  rebar sampling frame in a diamond-shaped configuration. The control pot was oriented upstream to prevent downstream nutrient contamination (Tate, 1990). The sampling frames were placed in the stream at both study reaches in pool habitats at water depths between 0.5 and 1.0 m. The pots were placed so that maximum sunlight (south-facing corridor through the riparian canopy) was realized. Forty sampling frames were placed in the stream during

each experiment, 20 at each reach. After 14 days, 20 of the sampling frames were removed (10 from each reach). After 35 days, the remaining frames were removed. Sample sizes were smaller in the summer (as indicated by the degrees of freedom reported in the Results section) because some of the sampling frames were disturbed by recreational stream users. Pots were placed in zip-lock bags, put on ice, transported to the lab and processed within 24 h of retrieval. Algae were scraped off the pot surface using a razor blade and a toothbrush. Samples were brought to constant volume, mixed with a magnetic stirrer, and sub-sampled for AFDM. The remainder of each sample was preserved in 4% formaldehyde for microscopic analysis. Algal composition was quantified by counting at least 500 cells from each sample. Biovolumes of each of the major taxa (taxa having 5% relative abundance or greater) were estimated by measuring the length and width of 10 randomly selected cells of each taxon.

Algal accrual data were analyzed using ANOVA with nutrient treatment and reach type as main effects. Algal community composition was compared between reaches, seasons and treatments using NMDS and MRPP analyses (McCune & Mefford, 1999).

We acknowledge that this design is pseudo-replicated and that statistical tests will tell us whether the two reaches differ in decomposition and algal accrual but will not directly test whether these differences are due to travertine formations (Hurlbert, 1984). Nevertheless, we believe that studies that document differences in ecological patterns associated with distinct geologic formations advance the field by generating hypothesis that can continue to be tested in other systems. Because geologic and ecological processes occur at such different time scales, fully replicated, controlled experiments are difficult to implement. We rarely observe such dramatic differences in stream morphology at two sites where climate and flow regimes are the same, making it reasonable to attribute differences in ecology to the extreme differences in morphology. We understand, however, the statistical limitations of this approach and will use statistical tests to determine if the two sites differ, acknowledging that differences may have resulted from factors other

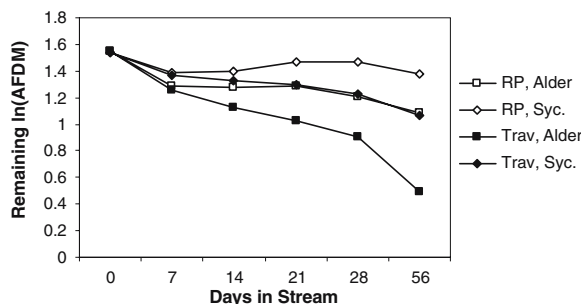
than travertine formation. This approach was recommended by Hurlbert (1984) when true replication is impossible. The return of full flows to Fossil Creek should increase travertine dams within the next decade. Results of this study will generate focused and testable hypotheses for how ecosystem processes will change as travertine dams become more prominent.

## Results

### Leaf litter decomposition

Leaf litter decomposed more quickly at the travertine dam forming reach (travertine reach) than at the riffle-pool reach for both alder and sycamore ( $p < 0.0001$ ; Fig. 2). Alder decomposed more quickly at both sites ( $p = 0.0001$ , Fig. 2) but decomposed three times faster at the travertine reach relative to the riffle-pool reach. The decomposition coefficient ( $k$ ) for alder at the travertine reach was  $0.018 (\pm 0.0006)$  but only  $0.007 (\pm 0.0007)$  at the riffle-pool reach. Sycamore decomposed 10 times more quickly ( $k = 0.008 \pm 0.0004$ ) at the travertine reach relative to the riffle-pool reach ( $k = 0.002, \pm 0.0006$ ). Significant reach to reach differences were evident by day 14 and continued for the duration of the experiment. There was no significant interaction between reach and species.

Differences in decomposition were accompanied by differences in macroinvertebrates collected from the leaf litterbags. After 14 days macroinvertebrates were more abundant at the



**Fig. 2** Mean ln(AFDM) by days in stream for both alder and sycamore (Syc.) at the travertine dam reach (Trav) and the riffle-pool reach (RP). Standard error bars are smaller than the height of the symbols in the graph

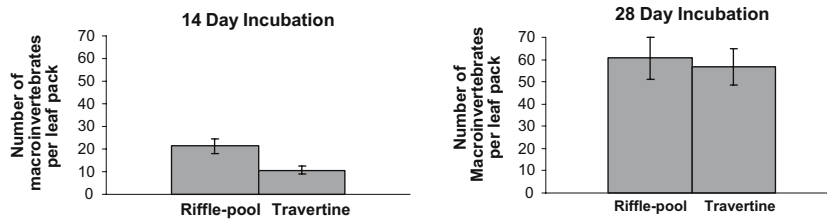
riffle-pool reach than the travertine reach ( $F = 9.12$ , 38 df,  $p = 0.0052$ ; Fig. 3). In contrast, macroinvertebrate diversity was greater after 14 days at the travertine reach with a Shannon Diversity Index ( $H'$ ) of 0.59 vs. 0.24 at the riffle-pool reach. After 28 days, the abundance of macroinvertebrates in the leaf litter did not differ between reaches (Fig. 3) although diversity continued to be higher at the travertine reach ( $H' = 0.66$ ) than the riffle-pool reach ( $H' = 0.19$ ).

The invertebrate community composition differed between reaches during both sampling periods (Fig. 4 and See Electronic Supplementary Material). In the 14-day incubation samples there was a moderately strong within reach grouping and a highly significant difference between reaches (MRPP:  $A = 0.078$ ;  $p = 0.0002$ ). Differences between the reaches were more pronounced by day 28 (MRPP:  $A = 0.176$ ;  $p < 0.0001$ , Fig. 4). For both sample dates, the travertine reach was distinguished from the riffle-pool reach by the presence of large numbers of snails (*Physella*, *Gyraulus*, and Hydrobiidae) as well as the damselfly *Argia* and the beetle *Microcylloepus*. In contrast, dominant taxa at the riffle-pool reach included chironomids, the mayfly *Baetis*, and the black fly larvae *Simulium* (Fig. 4 and See Electronic Supplementary Material).

### Algal accrual

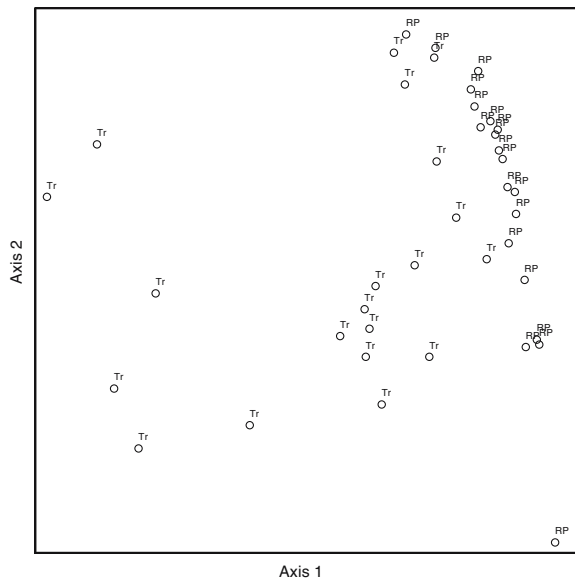
Algae accrued more quickly at the travertine reach than the riffle-pool reach during all three seasons (Fig. 5). In the fall, differences between the reaches were evident by day 35 when algal accrual was two times greater at the travertine reach ( $F = 12.41$ , 19 df,  $p = 0.0022$ ; Fig. 5). During the winter, differences were apparent by day 14 ( $F = 22.57$ , 18 df,  $p = 0.0002$ ; Fig. 5). Differences between the reaches were most dramatic in the summer when the control substrates in the travertine reach had over 21 times as much algae as the control substrates collected from the riffle-pool reach ( $F = 167.05$ , 6 df,  $p < 0.0001$ ; Fig. 5).

Algae did not respond to nutrient enrichment at the riffle-pool reach during any season. In contrast, at the travertine reach algae responded to enrichment in the fall and summer (Fig. 6). In the fall, algae responded to nitrogen enrichment



**Fig. 3** Comparison of mean total abundance of macroinvertebrates (all species combined) per leaf pack between travertine and riffle-pool reaches for the 14 day incubation and the 28 day incubation

by day 35 ( $F = 5.91$ , 18 df,  $p = 0.027$ ; Fig. 6). In the early summer, algal growth was higher on the nitrogen + phosphorous treatments relative to other treatments by day 14 ( $F = 52.32$ , 8 df,  $p < 0.0001$ ). On day 35 algae responded to nitrogen ( $F = 41.14$ , 8 df,  $p = 0.0002$ ), phosphorous ( $F = 26.49$ , 8 df,  $p = 0.0009$ ), and nitrogen + phosphorous ( $F = 42.41$ , 8 df,  $p < 0.0001$ ) with highest biomass on the nitrogen + phosphorous treatments indicating co-limitation of nitrogen and phosphorus. There were no differences in algal accrual across nutrient treatments in the winter after 14 days. The winter 35-day substrates were lost in a flood.

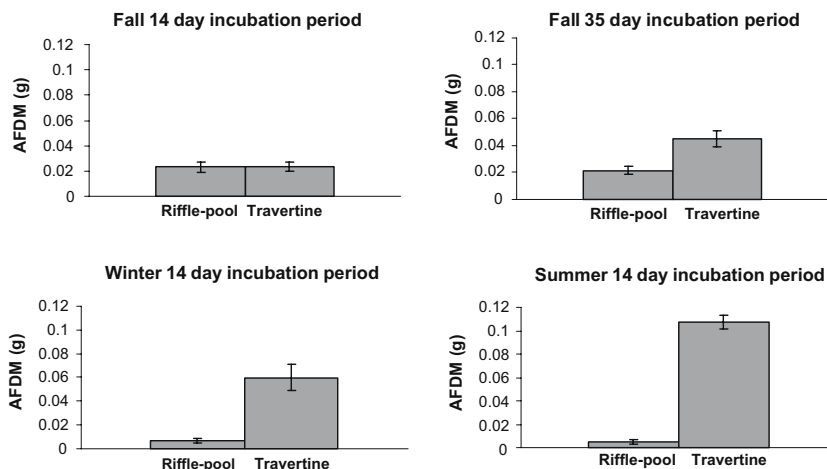


**Fig. 4** Non Metric Dimensional Scaling (NMDS) ordination of macroinvertebrate community composition samples taken at the travertine dam reach (Tr) and the riffle-pool reach (RP) for the 28 day incubation period. Samples having similar macroinvertebrate community composition are grouped closer together

Algal community composition differed significantly between the two reaches during the fall (MRPP:  $A = 0.1107$ ;  $p = 0.0007$ ), winter (MRPP:  $A = 0.6457$ ;  $p < 0.0001$ ), and summer (MRPP:  $A = 0.4723$ ;  $p < 0.0001$ ). Algal assemblages differed across seasons at both sites (See Electronic Supplementary Material). Nutrient enrichment did not affect community composition at either site. In general, filamentous algae dominated the travertine reach whereas single celled diatoms dominated the riffle-pool reach (See Electronic Supplementary Material). Dominant taxa in the travertine reach included *Vaucheria*, *Spirogyra*, *Oscillatoria* and *Cladophora glomerata* (L.) Kütz. In contrast, diatoms dominated the riffle-pool reach: *Anomoeoneis*, *Stauroneis*, *Fragilaria*, *Cymbella*, *Gomphonema*, *Synedra*, and *Amphora*. These diatoms constituted 80–90% of the algal assemblage at the riffle-pool reach (See Electronic Supplementary Material).

## Discussion

Decomposition and algal accrual were accelerated in the travertine reach relative to the riffle-pool reach. This is in contrast to other travertine streams, where travertine deposition on leaves reduced decomposition (Casas & Gessner, 1999). The discrepancy between these studies could be due to differences in the type of travertine deposition. Casas & Gessner (1999) described a continuous layer of travertine covering the stream bottom. This type of marl deposition, or armoring of the substrate, is likely to impede decomposition directly by making the substrate physically inaccessible. However, such substrate armoring was not observed in the active travertine dam forming

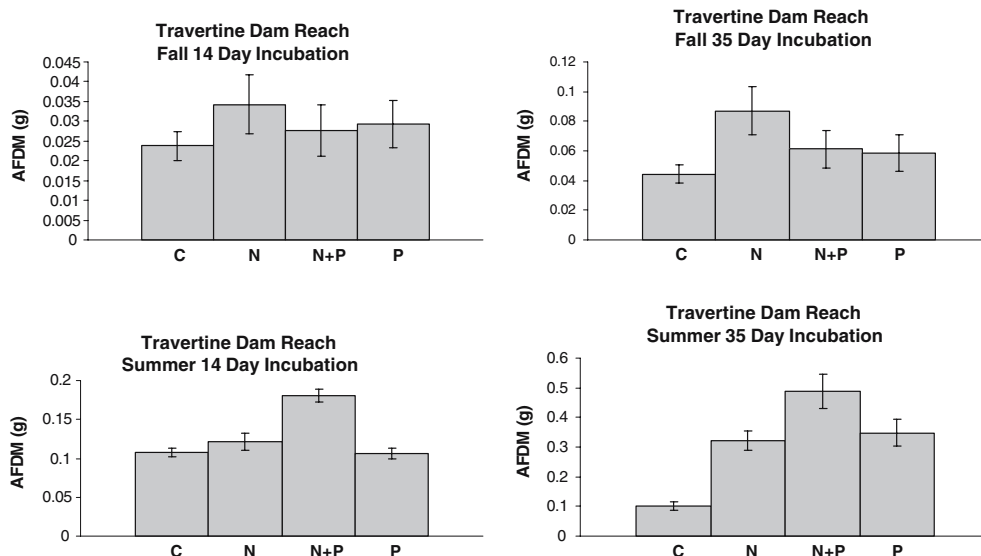


**Fig. 5** Comparisons of mean algal accrual (AFDM) for the control treatment at the riffle-pool and travertine dam reaches

reach of Fossil Creek where travertine preferentially deposited on dams and did not cover the stream bottom in the pool areas between dams. During site visits in the fall, leaf litter was observed sticking to the travertine dam surfaces and being cemented into the travertine dams; however the vast majority of the leaf litter was observed being retained on the upstream side of the travertine dams. Thick layers of leaf material (measuring up to 0.5 m deep) were deposited on the stream bottom immediately upstream of the

travertine structures. In contrast, at the riffle-pool reach leaf litter settled out into smaller, more widely dispersed packs along the stream margins, at the downstream ends of pools, and in the eddies in riffles. Though not quantified, it is likely that much more leaf litter was retained in the travertine reach relative to the riffle-pool reach.

Elevated decomposition and algal accrual in the travertine reach may be due to a combination of factors including higher temperatures (leaf litter, Bird & Kaushik, 1981; algal accrual,



**Fig. 6** Comparisons among nutrient treatments for the travertine dam reach, during the fall and summer harvest dates (C = Control; N = Nitrogen; N + P = Nitrogen + Phosphorous; P = Phosphorous)



DeNicola, 1996), higher water clarity (Waters, 1995), tighter nutrient cycling (McClain et al., 2003) and a different trophic structure (Power et al., 1996; Marks et al., 2000). Because of the pseudoreplication inherent in this design we reiterate that the differences between the sites may not be due to travertine formation. We argue however, that due to the profound effects of travertine deposition on stream morphology and components of stream chemistry, travertine directly or indirectly affects many of the other putative variables that could be driving these trends.

Higher water temperatures at the travertine site during the winter almost certainly contributed to elevated leaf litter decomposition (Bird & Kaushik, 1981) and algal accrual (DeNicola, 1996). Although an important physiological driver, temperature cannot be the only variable causing these differences because differences in algal accrual were most pronounced during the summer when temperatures were similar between the sites. Additional studies in Fossil Creek show that reach scale primary productivity and respiration are higher at the travertine site during all seasons – differences that are not correlated with temperature (Gibson and Marks unpublished data).

The higher levels of nitrogen and phosphorus at the travertine site may have also increased decomposition (Boulton & Boon, 1991) and algal growth (Allan, 1995; Pringle, 1987; Grimm & Fisher, 1986). If nutrients were the primary factor limiting algal accrual however, we would have expected a stronger response to fertilization at the riffle-pool site. The lack of response to nutrient enrichment at the riffle-pool site argues that factors other than nutrient levels caused the differences in algal accrual between the sites. Water chemistry differences are likely due to in-stream processes because there are no major tributaries entering the river between the two sites. In the summer algae in the travertine reach were limited by nitrogen, phosphorus, and co-limited by nitrogen and phosphorus. Although calcium can bind phosphorus making it unavailable to algae (Wetzel, 2001), we postulate that tight nutrient cycling on the travertine dams themselves may be binding and releasing phos-

phorus, accounting for the higher phosphate concentrations in the water column. Similarly, cyanobacteria associated with travertine may be fixing nitrogen at rates high enough to increase nitrogen concentrations in the pools between the dams. This “hot spot” hypothesis would need to be tested using small scale experiments comparing nitrogen fixation and nutrient cycling on travertine dams with other sites in the stream (McClain et al., 2003).

Another notable difference between the two study reaches was that there was more fine sediment deposited on the leaf litterbags and algal substrates at the riffle-pool site. Fine sediment functions as a broad based metabolic inhibitor by coating biologically active surfaces (Waters, 1995). Deposited fine sediment can slow down leaf litter processing rates (Reice, 1974). Drifting macroinvertebrates will also avoid substrates that are coated with sediment (Ciborowski et al., 1977). Suspended sediments can reduce photosynthesis (Lewis, 1998) and deposited sediments can coat or smother benthic algae (Waters, 1995). We did not directly measure sediment loads in the two sites and it is likely that sediment inputs are higher downstream. We did observe high sediment loads in the benthos in the deep pools in the travertine reach, although sediment did not cover the artificial substrates. We postulate that travertine traps sediments in several ways. First, the travertine matrix may act as a sieve, locking up suspended sediments as the water flows over the travertine dams. Second, thick growths of the green alga, *Cladophora glomerata*, are often associated with the travertine dams at Fossil Creek, likely function as biological sediment traps (Dodds & Gudder, 1992). Finally, between dams, the abundant algae on the stream bottom may stabilize this sediment.

Although these two sites are only 6 km apart, the food webs are dramatically different. The large pools in the travertine reach support significantly higher fish biomass and lower grazer biomass, despite higher invertebrate diversity (Marks et al., 2006). The increased rates of algal accrual and the large algal mats observed in the travertine reach may be a result of trophic control where predators suppress grazers, releasing algae from herbivory creating a three level food chain

in the travertine reach versus a two level food chain in the riffle-pool reach (*sensu* Power et al., 1996; Marks et al., 2000).

### Implications

The algal nutrient limitation portion of this study has useful land management implications. The growth release observed at the travertine reach in the summer months for the N + P treatment is substantial – a nearly 5 fold increase when compared with control substrates. Approximately 2200 day hikers and 1000 campers visit the Fossil Springs area each year (USFS, 2002). With the return of full flows to Fossil Creek it is likely recreational use will increase. At present, there are no restroom facilities near the river. Humans release ~12 g of nitrogen and 1.5 g of phosphorous per person per day through human waste (Kalff, 2002). Food particles and detergents that may enter the stream through camping activities can also contribute phosphorous. The steep canyon bound terrain of Fossil Creek focuses recreational use into a narrow riparian corridor. Spates in southwestern streams are common and may wash human waste in to the stream. Nutrient rich waters can produce nuisance level blooms of algae where aesthetics and stream recreation are negatively impacted (Biggs, 1996). Filamentous green algae such as *Ulothrix*, *Cladophora*, and *Rhizoclonium*, all present in Fossil Creek, can grow up to several meters in length. Biomass of green algae above 55% cover can seriously degrade ecosystem function by smothering the substrate (Biggs, 1996).

One of the main goals of the Fossil Creek restoration project is to restore a native fish assemblage (USFS, 2004). The native fish assemblage of Fossil Creek consists of roundtail chub *Gila robusta* Baird & Girard, headwater chub *Gila nigra* Cope, speckled dace *Rhinichthys osculus* Girard, longfin dace *Agosia chrysogaster* Girard, desert sucker *Catostomus clarki* Baird & Girard, and Sonora sucker *Catostomus insignis* Baird & Girard (AGFD, 1996). Historically these fishes occurred throughout Fossil Creek, but in more recent times they have been severely reduced in abundance and distribution (USFS, 2004). If travertine dams increase in size and ex-

tent with the return of full flows as predicted, our results predict concurrent increases in autochthonous (algae) and allochthonous (detritus) energy available to higher trophic levels. Increased algal accrual will directly benefit the diets of several species of native fish. Algae are a major component in the diets of both of the sucker species (Clarkson & Minckley, 1988) and the early life stages of the chub species (Neve, 1976). Algae are also consumed by speckled dace (Greger & Deacon, 1988), and longfin dace (Sublette et al., 1990). The algal community composition at the travertine site had a much higher percentage of filamentous taxa. This could be beneficial for native fishes because it was filamentous algae found in diets of roundtail chub (Bestgen, 1985) and longfin dace (Sublette et al., 1990), while Kobetich (1969) found both filamentous algae and diatoms in the diet of desert sucker with filamentous green algae being the primary food source. Detritus is a major component in the diet of longfin dace (Sublette et al., 1990) and is directly consumed by both sucker species (Clarkson & Minckley, 1988; Kobetich, 1969) and to a lesser extent speckled dace (Greger & Deacon, 1988). Macroinvertebrates are consumed by all native fish species in Fossil Creek (Sublette et al., 1990), and make up the largest component of the diet of adult chubs (Neve, 1976; Bestgen, 1985) and speckled dace (Greger & Deacon, 1988). The occurrence of higher macroinvertebrate numbers in the leaf litterbags during the fall season at the riffle-pool reach may apparently support the hypothesis of food limitation in the presence of travertine formation; however, the macroinvertebrates at the riffle-pool reach consisted mostly of smaller bodied chironomids, while the travertine contained a greater number of larger bodied taxa such as snails and damselflies. Therefore, it's likely that a greater biomass of macroinvertebrates was present in leaf litter at the travertine reach. Also, the likelihood of greater retention of leaf litter at the travertine reach should translate into a greater biomass of leaf litter and a greater overall abundance of macroinvertebrates in leaf litter. The greater diversity of macroinvertebrates found in leaf litter at the travertine reach may also yield a wider array of food sources for native fishes. In samples

taken from a variety of habitats in Fossil Creek macroinvertebrate densities were similar, and species richness was greater, at the travertine dam forming reach relative to other reaches (Marks et al., 2006). In summary, the greater algal accrual, faster leaf litter decomposition, higher macroinvertebrate diversity, and likely greater leaf litter retention at the travertine site suggests that there will be a greater abundance of food resources available for native fishes with an increase in travertine dam formation. This is in contrast to our initial predictions and concerns by managers that fish will become food limited as travertine deposition increases.

This study and other published studies on Fossil Creek (Overby & Neary, 1996; Malusa et al., 2003; Marks et al., 2006) provide distinct predictions about how geomorphic and ecological processes will change with increased flow. In the decades to come this system will provide a unique opportunity to test experimentally interactions and feedbacks between ecological and geomorphic processes in travertine ecosystems.

## References

- AGFD (Arizona Game and Fish Dept.), 1996. Fossil Creek Management Report. Federal aid project F-7-M-38. Arizona Department of Game and Fish, Phoenix.
- Allan, J. D., 1995. Stream Ecology: Structure and Function of Running Waters. Chapman and Hall, London.
- Barnes, I., 1965. Geochemistry of Birch Creek, Inyo County, California – a travertine depositing creek in an arid climate. *Geochimica Et Cosmochimica Acta* 29: 85–112.
- Benfield, E. F., 1996. Leaf breakdown in stream ecosystems. In Hauer, F. R. & G. A. Lamberti (eds), *Methods in Stream Ecology*. Academic Press, San Diego, California.
- Bestgen, K. R., 1985. Distribution, biology, and status of the roundtail chub, *Gila robusta*, in the Gila River Basin, New Mexico. M.S. Thesis, Colorado State University, Fort Collins.
- Biggs, B. J., 1996. Patterns in benthic algae in streams. In Stevenson, R. J., M. L. Bothwell & R. L. Lowe (eds), *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press, San Diego, California.
- Biondini, M. E., C. D. Bonham & E. F. Redente, 1985. Secondary successional patterns in a sagebrush (*Artemisia tridentata*) community as they relate to soil disturbance and soil biological activity. *Vegetatio* 60: 25–36.
- Bird, G. A. & N. K. Kaushik, 1981. Coarse particulate organic matter in streams. In Lock, M. A. & D. D. Williams (eds), *Perspectives in Running Water Ecology*. Plenum Press, New York.
- Boulton, A. J. & P. I. Boon, 1991. A review of methodology used to measure leaf litter decomposition in lotic environments: Time to turn over and old leaf? *Australian Journal of Marine and Freshwater Research* 42: 1–43.
- Cacchio, P., C. Ercol, G. Cappuccio & A. Lepidi, 2003. Calcium carbonate precipitation by bacterial strains isolated from a limestone cave and from a loamy soil. *Geomicrobiology Journal* 20: 85–98.
- Casas, J. J., J. Picazo & M. L. Carcelen, 1994. Leaf packs breakdown in a karstic Mediterranean stream. *Verhandlungen Internationale Vereinigung für Limnologie* 25: 1739–1744.
- Casas, J. J. & M. O. Gessner, 1999. Leaf litter breakdown in a Mediterranean stream characterized by travertine precipitation. *Freshwater Biology* 41: 781–793.
- Ciborowski, J. J. H., P. J. Pointing & L. D. Corkum, 1977. The effect of current velocity and sediment on the drift of the mayfly *Ephemerella subvaria* McDunnough. *Freshwater Biology* 7: 567–572.
- Chamberlain, F. M., 1904. Notes on Work in Arizona – 1904. Unpublished report on file with the Smithsonian Institution Archives, Washington, D.C.
- Clarkson, R. W. & W. L. Minckley, 1988. Morphology and foods of Arizona catostomid fishes: *Catostomus insignis*, *Pantosteus clarki*, and their putative hybrids. *Copeia* 1988: 422–433.
- D'Angelo, D. J., J. R. Webster, S. V. Gregory & J. L. Meyer, 1993. Transient storage in Appalachian and Cascade mountain streams as related to hydraulic characteristics. *Journal of the North American Benthological Society* 12: 223–235.
- DeNicola, D. M., 1996. Periphyton responses to temperature at different ecological levels. In Stevenson R. J., M. L. Bothwell & R. L. Lowe (eds), *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press, San Diego, California.
- Dinger, E. C., 2001. Aquatic invertebrates of Cuatro Ciénegas, Coahuila, México and effects of fish on stromatolite invertebrate assemblages. M.S. Thesis, Northern Arizona University, Flagstaff.
- Dodds, W. K. & D. A. Gudder, 1992. The ecology of *Cladophora*. *Journal of Phycology* 28: 415–427.
- Dokuchaev V.V., 1883. Russian Chernozems (Russkii Chernozems). Israel Program for Scientific Translations 1967. Translated from Russian by N. Kaner. Available from U.S. Dept. of Commerce, Springfield, VA.
- Doyle, M. W., E. H. Stanley & J. M. Harbor, 2003. Hydrogeomorphic controls on phosphorus retention in streams. *Water Resources Research* 39: 1147–1163.
- Drysdale, R. N., 1999. The sedimentological significance of hypsychid caddis-fly larvae (Order: Trichoptera) in a travertine-depositing stream: Louie Creek, Northwest Queensland, Australia. *Journal of Sedimentary Research* 69: 145–150.

- Emeis, K. C., H. H. Richnow & S. Kempe, 1987. Travertine formation in Plitvice National Park, Yugoslavia: Chemical versus biological control. *Sedimentology* 34: 595–609.
- Fairchild, G. W. & R. L. Lowe, 1984. Artificial substrates which release nutrients: Effects on periphyton and invertebrate succession. *Hydrobiologia* 114: 29–37.
- FERC (Federal Energy Regulatory Commission), 1997. Draft Environmental Assessment For Hydropower License: Childs Irving Project, FERC Project No. 2069–003 Arizona.
- Freyet P. & E. P. Verrecchia, 1998. Freshwater organisms that build stromatolites: A synopsis of biocrystallization by prokaryotic and eukaryotic algae. *Sedimentology* 45: 535–563.
- Golubic, S., 1973. The relationship between blue-green algae and carbonate deposits. In: Carr N. G. & B. A. Whitton (eds), *The Biology of Blue-Green Algae*. Blackwell Scientific, Oxford, 434–472.
- Golubic, S., L. Seong-Joo, & K. M. Brown, 2000. Cyanobacteria: Architects of sedimentary structures. In Riding, R. & S. M. Awramik (eds) *Microbial Sediments*, Springer-Verlag, Heidelberg, Berlin, New York.
- Greger, P. D. & J. E. Deacon, 1988. Food partitioning among fishes of the Virgin River. *Copeia* 1988: 314–323.
- Grimm, N. B. & S. G. Fisher, 1986. Nitrogen limitation in a Sonoran Desert stream. *Journal of the North American Benthological Society* 5: 2–15.
- Hurlbert, S. H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Jenny, H., 1941. *Factors of Soil Formation*. McGraw-Hill Publishers, New York.
- Kalff, J., 2002. *Limnology*. Prentice-Hall, Upper Saddle River, NJ.
- Kobetich, G. C. 1969. The food habits of the Gila mountain-sucker *Pantosteus clarki*. M.S. Thesis, University of New Mexico, Albuquerque.
- Lewis, W. M., 1998. Primary production in the Orinoco River. *Ecology* 69: 679–692.
- LeRoy, C. J., & J. C. Marks, 2006. Litter quality, stream condition, and litter diversity influence decomposition rates and macroinvertebrate communities. *Freshwater Biology* 51: 605–617.
- Malusa, J., S. T. Overby & R. A. Parnell, 2003. Potential for travertine formation: Fossil Creek, Arizona. *Applied Geochemistry* 18: 1081–1093.
- Marks J. C., M. E. Power & M. S. Parker, 2000. Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos* 90: 20–27.
- Marks, J. C., R. Parnell, C. D. Carter, E. C. Dinger & A. Haden, 2006. Interactions between geomorphology and ecosystem processes in travertine streams – implications for dam decommissioning in Fossil Creek, Arizona. *Ecological Applications*, in review.
- McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, E. Mayorga, W. H. McDowell & G. Pinay, 2003. Biogeochemical hot spots and hot moments at the interface of aquatic and terrestrial ecosystems. *Ecosystems* 6: 301–312.
- McCune, B. & M. J. Mefford, 1999. *PC-ORD. Multivariate Analysis of Ecological Data*. MJM Software Design, Gleneden Beach, Oregon, USA.
- Merritt, R. W. & K. W. Cummins, 1996. *An Introduction to the Aquatic Insects of North America*, 3rd edn. Kendall-Hunt Publishing Company, Dubuque, Iowa, USA.
- Mielke P. W. Jr., 1984. Meteorological applications of permutation techniques based on distance functions. In Krishnaiah, P. R. & P. K. Sen (eds), *Handbook of Statistics*. Elsevier Scientific Publishers, New York.
- Minckley, W. L. & J. E. Deacon, editors. 1991. *Battle Against Extinction: Native Fish Management in the American West*. University of Arizona Press, Tucson).
- Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing & R. L. Vannote, 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* 53: 1–25.
- Neve, L. C., 1976. The life history of the roundtail chub, *Gila robusta grahami*, at Fossil Creek, Arizona. M.S. Thesis, Northern Arizona University, Flagstaff.
- Oberlin, G. E., J. P. Shannon & D. W. Blinn, 1999. Watershed influence on the macroinvertebrate fauna of ten major tributaries of the Colorado River through Grand Canyon, Arizona. *The Southwestern Naturalist* 44: 17–30.
- Overby, S. T. & D. G. Neary, 1996. Travertine Geomorphology of Fossil Creek. Hydrology Section, Arizona–Nevada Academy of Science. 16: 9–12.
- Pentecost, A., 2003. Cyanobacteria associated with hot spring travertines. *Canadian Journal of Earth Science* 40: 1447–1457.
- Power M. E., M. S. Parker & J. T. Wootton, 1996. Disturbance and food chain length in rivers. In Polis, G. A. & K. O. Winemiller (eds), *Food Webs: Integration of Patterns and Dynamics*. Chapman and Hall, pp 286–297.
- Pringle, C. M., 1987. Effects of water and substratum nutrient supplies on lotic periphyton growth: An integrated bioassay. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 619–629.
- Reice, S. R., 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. *Ecology* 55: 1271–1282.
- Rinne, J. N. & W. L. Minckley. 1991. Native fishes of arid lands: A dwindling resource of the desert Southwest. Gen. Tech. Rep. RM-206. Ft. Collins, CO: U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station.
- Stumm, W., & J. J. Morgan, 1970. *Aquatic Chemistry: An Introduction Emphasizing Chemical Equilibria in Natural Waters*. Wiley-Interscience, New York.
- Sublette, J. E., M. Sublette & M. D. Hatch, 1990. *Fishes of New Mexico*. University of New Mexico Press, Albuquerque.
- Tate, C. M., 1990. Patterns and controls of nitrogen in tallgrass prairie streams. *Ecology* 71: 2007–2018.
- Thorpe, J. H. & A. P. Covich, 2001. *Ecology and Classification of North American Fresh Water Invertebrates*, 2nd edn. Academic Press, San Diego, California, USA.

- USFS (US Forest Service), 2002. Proposed action for Fossil Creek Planning Area. US Forest Service, Coconino National Forest, Arizona.
- USFS (US Forest Service), 2004. Final Environmental Assessment Native Fish Restoration in Fossil Creek. Forest Service, Southwest Region.
- USFWS (US Fish and Wildlife Service), 2003. Apache Trout Recovery Plan, Second Revision. Albuquerque, New Mexico.
- USFWS (US Fish and Wildlife Service), 2005. Endangered and Threatened Wildlife and Plants. 50 CFR 17.11 and 17.12, November 2005.
- Valett, M. E., J. A. Morrice, C. N. Dahm & M. E. Campana, 1996. Parent lithology, surface-groundwater exchange, and nitrate retention in headwater streams. *Limnology and Oceanography* 41: 333–345.
- Vannote, R. L., G. W. Minshall & K. W. Cummins, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.
- Waters, T. F., 1995. *Sediment in Streams*. American Fisheries Society Monograph 7. American Fisheries Society. Bethesda, Maryland.
- Warren, L. A., P. A. Maurice, F. Nagina Parmar & F. Grant Ferris, 2001. Microbially mediated calcium carbonate precipitation: Implications for interpreting calcite precipitation and for solid-phase capture of inorganic contaminants. *Geomicrobiology* 18: 93–115.
- Webster, J. R. & E. F. Benfield, 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics*. 17: 567–594.
- Wetzel, R. G., 2001. *Limnology: Lake and River Ecosystems*. 3rd edn. Academic Press, New York.
- Wiggins, G. B., 1996. *Larvae of the North American Caddisfly Genera (Trichoptera)*, 2nd edn. University of Toronto Press, Toronto, Ontario, Canada.
- Zhang, C. L., B. W. Fouke, G. Bonheyo, A. Peacock, D. C. White, Y. Huang & C. S. Romanek, 2004. Lipid biomarkers and carbon-isotopes of modern travertine deposits (Yellowstone National Park, USA): Implications for biogeochemical dynamics in hot-spring systems. *Geochimica Et Cosmochimica Acta* 68: 3157–3169.