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Ecogeomorphic feedbacks in regrowth of travertine step-pool morphology after dam decommissioning, Fossil Creek, Arizona

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ABSTRACT

The linkages between fluvial geomorphology and aquatic ecosystems are commonly conceptualized as a one-way causal chain in which geomorphic processes create the physical template for ecological dynamics. In streams with a travertine step-pool morphology, however, biotic processes strongly influence the formation and growth of travertine dams, creating the potential for numerous feedbacks. Here we take advantage of the decommissioning of a hydroelectric project on Fossil Creek, Arizona, where restoration of $CaCO_3$-rich baseflow has triggered rapid regrowth of travertine dams, to explore the interactions between biotic and abiotic factors in travertine morphodynamics. We consider three conceptual frameworks, where biotic factors independently modulate the rate of physical and chemical processes that produce travertine dams; combine with abiotic factors in a set of feedback loops; and work in opposition to abiotic processes, such that the travertine step-pool morphology reflects a dynamic balance between dominantly-biotic constructive processes and dominantly-abiotic destructive processes. We consider separately three phases of an idealized life cycle of travertine dams: dam formation, growth, and destruction by erosive floods. Dam formation is catalyzed by abiotic factors (e.g. channel constrictions, and bedrock steps) and biotic factors (e.g. woody debris, and emergent vegetation). From measurements of changes over time in travertine thickness on a bedrock step, we find evidence for a positive feedback between flow hydraulics and travertine accrual. Measurements of organic content in travertine samples from this step show that algal growth contributes substantially to travertine accumulation and suggest that growth is most rapid during seasonal algal blooms. To document vertical growth of travertine dams, we embedded 252 magnets into nascent travertine dams, along a 10 km stretch of river. Growth rates are calculated from changes over time in the magnetic field intensity at the dam surface. At each magnet we record a range of hydraulic and travertine composition variables to characterize the dominant mechanism of growth: abiotic precipitation, algal growth, trapping of organic material, or *in situ* plant growth. We find: (1) rapid growth of travertine dams following flow restoration, averaging more than 2 cm/year; (2) growth rates decline downstream, consistent with loss of dissolved constituents because of upstream travertine deposition, but also parallel to a decline in organic content in dam surface material and a downstream shift in dominant biotic mechanism; (3) biotic mechanisms are associated with faster growth rates; and (4) correlations between hydraulic attributes and growth rates are more consistent with biotic than abiotic controls. We conclude that the strong influence of living organisms on rates of travertine growth, coupled with the beneficial effects of travertine on ecosystem dynamics, demonstrate a positive feedback between biology and geomorphology. During our two-year study period, erosive flood flows occurred causing widespread removal of travertine. The temporal distribution of travertine growth and erosion over the study period is consistent with a bimodal magnitude–frequency relation in which growth dominates except when large, infrequent storms occur. This model may be useful in other systems where biology exerts strong controls on geomorphic processes.

1. Introduction

At a planetary scale, Earth surface morphodynamics are influenced by the interaction of living organisms with abiotic physical and chemical processes and materials. Life exists on Earth in part because abundant water is present in the liquid phase (Schwartzman, 2002). The course of the proliferation of life and its evolution has been profoundly influenced by geologic events, from the slow shifting of continents (Brown and Lomolino, 1998) to sudden extraterrestrial impacts (Benton and Twitchett, 2003). Living organisms in turn affect the surface in myriad ways, from the creation of free oxygen in the atmosphere in the Archean to the ubiquitous and transformative effects of human activities today (Vitousek et al., 1997; Hooke, 2000).

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Do the strong interactions of life and its abiotic environment extend down to the scale of individual river channels? Although an emerging literature focuses on dynamic interactions between life and landscape morphodynamics (e.g. Corinblit et al., 2007; Reinhardt et al., 2010), most previous work on the linkages between life and fluvial geomorphology has focused primarily on the role of the physiochemical processes in setting the template for biological processes (Vannote et al., 1980; Minshall et al., 1983; Doyle et al., 2003). In the field of river restoration, a useful conceptual model for a five-component chain of causality (Fig. 1; Stillwater Sciences, 2001) begins with (1) the supply of materials (e.g. water, sediment, and nutrients), which drive (2) the geomorphic processes (e.g. erosion, and transport and deposition of sediment), which lead to (3) formation of characteristic landforms (e.g. bars, pools, and floodplains). These morphologic units provide (4) habitat for various life cycle stages of species of concern (e.g. spawning, rearing, and over-wintering for salmonids), the quality of which helps determine (5) the population and community responses (e.g. species abundance, diversity, and trophic complexity). Although this systems perspective provides a framework for understanding how biota respond to the abiotic environment, the assumed one-way direction of influence does not incorporate the possibility of feedbacks between biotic and abiotic processes in driving fluvial morphodynamics, for example the effect of riparian vegetation on bank strength, channel width and rates of bank erosion (e.g., Gurnell, 1995; Micheli and Kirchner, 2002) (Fig. 1).

Dietrich and Perron (2006) posed the question of whether a topographic signature to life exists and concluded that although living organisms often play essential roles in shaping landforms, life may impart only a statistical tendency favoring certain topographic outcomes over others; however, the full range of possible topographic outcomes could arise without the participation of life. For example, the contribution of riparian vegetation to bank strength may make channels narrower (Hey and Thorne, 1986), but narrow channels with strong banks also occur because of clay-rich or bedrock bank material. Consideration of the potential for feedbacks between biotic and abiotic processes suggests that the role of life may be most clearly discerned in the dynamics of fluvial systems, rather than in a static measure of channel form.

Travertine streams, where active $CaCO_3$ precipitation from supersaturated spring-fed baseflow creates a characteristic step-pool morphology, provide an excellent model system to investigate complex interactions between biology and geomorphology. Travertine streams occur in a wide variety of climatic and geomorphic settings; in his comprehensive monograph on travertine, Pentecost (2005) identifies more than 100 studied travertine streams, distributed across six continents. Biological processes affect travertine growth across a wide range of scales (e.g. Emeis et al., 1989; Pedley, 1992; Pentecost, 2003, 2005). At the channel scale, log jams and other large woody debris (LWD) catalyze travertine dam formation by causing high-velocity overflow, which accelerates CO_2 outgassing and calcite deposition (Viles and Pentecost, 1999). On the crests of travertine dams, surface area for travertine precipitation is provided by the trapping of floating algal mats and leaf litter, and by *in situ* growth of algae and emergent macrophytes (Merz-Preis and Riding, 1999). At the scale of individual mineral crystals, microbial respiration lowers local pH, enhancing precipitation rates (Takashima and Kano, 2008). Travertine step-pool morphology, in turn, can have a strong positive influence on ecosystem processes. Recent work in Fossil Creek, Arizona, has shown that significantly higher rates of primary production, respiration, and nutrient retention occur within travertine reaches, compared to the non-travertine riffle-pool morphology along the same stream (Marks et al., 2006; Carter and Marks, 2007; Compson et al., 2009).

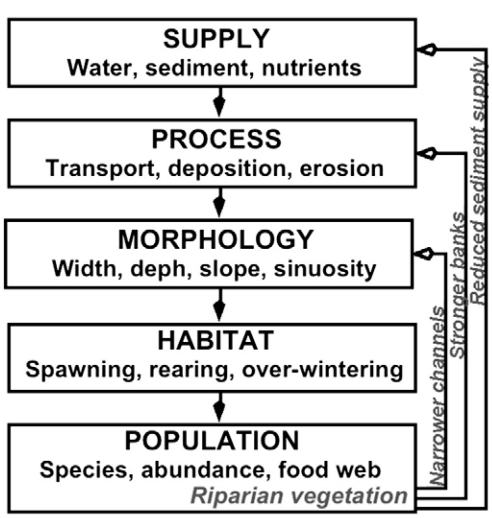

Fig. 1. Conceptual chain of causality linking abiotic watershed and channel conditions to biological responses. One-way linear model does not account for feedbacks, such as effect of riparian vegetation on bank erosion and channel width (modified from Stillwater Sciences, 2001).

In this study we take advantage of the recent decommissioning of a hydroelectric diversion dam on Fossil Creek, and the restoration of perennial $CaCO_3$-rich baseflow, to explore the biotic and abiotic influences on the rapid formation and growth of travertine dams. Using two years of measurements of travertine growth and erosion, combined with measures of morphologic and biologic conditions, at more than 250 locations, we find evidence for a set of positive feedbacks driving rapid geomorphic change.

In this paper we have used a somewhat unconventional structure. We begin by introducing the Fossil Creek field site, so that we can then use the dynamics of this particular river system to motivate three distinct frameworks for conceptualizing feedbacks and other interactions between biotic and abiotic processes. In the following three sections, we apply those three conceptual frameworks to an idealized life cycle of a travertine dam: first dam formation, then dam growth, and finally dam destruction by erosive floods. In each of these three sections we report the relevant field and analytic methods followed directly by the corresponding results and interpretations. In the discussion section we focus on the implications of our findings for understanding ecogeomorphic feedbacks in fluvial morphodynamics, including applications to river restoration.

2. Fossil creek study site

Fossil Creek is a tributary to the Verde River in central Arizona (Fig. 2A), and has cut a deep canyon into the Mogollon Rim, the southwestern edge of the Colorado plateau. Perennial and steady baseflow of ~1200 l/s (Feth and Hem, 1962; Malusa et al., 2003) discharges from seven springs located ~22 km upstream of the confluence with the Verde (Fig. 2B). Upstream of the springs, the channel is dry except during monsoonal and winter storms and a brief spring snow-melt. Downstream of the springs, the baseflow supports a lush corridor of riparian vegetation, bounded by steep and arid hillslopes. The spring-fed baseflow has high concentrations of dissolved calcium and bicarbonate ions, which precipitate as calcite as outgassing of dissolved CO_2 creates high levels of super-saturation (Malusa et al., 2003). The Martin formation below the Redwall limestone is a major source of the calcium carbonate-bearing groundwater (Feth and Hem, 1962), with dissolution driven in part by mantle-derived CO_2 (Crossey et al., 2006). Bedrock exposed in the channel bed and canyon walls includes Paleozoic sedimentary rocks of the Supai group and Coconino sandstone, and Cenozoic volcanic rocks, including basaltic lava and tuff from repeated flows into the pre-existing Fossil Creek canyon (Twenter, 1962; Feth and Hem, 1962; Blakey, 1990).

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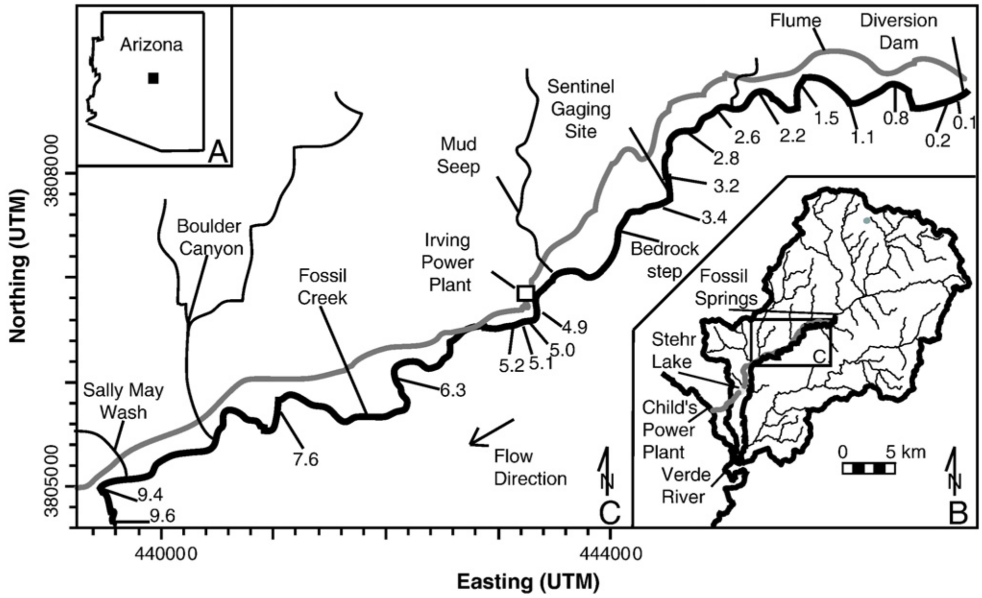

Fig. 2. Fossil Creek study area. A) Location within Arizona, B) Fossil Creek watershed, C) study area showing major tributaries, the hydroelectric infrastructure (diversion dam, Irving power plant and flume), bedrock step study site, flow gaging site, and magnet installation sites labeled by 'station' (distance downstream from the diversion dam measured along valley axis, in km). Minor ticks in 200 m increments; datum is UTM NAD 27 zone 12.

In 1909, an 8 m high dam was built across Fossil Creek (Fig. 3A), 0.6 km downstream of the springs, and the entire baseflow was diverted through a flume system primarily for hydropower generation at the Childs plant on the Verde River (Fig. 2B). A smaller power plant was also built along the Fossil Creek flume system, at Irving, ~5 km downstream of the diversion dam (Fig. 2C). The Irving plant generated power from ~12% of the diverted baseflow (~150 l/s), which was then returned to the creek; the rest of the diverted baseflow (~1050 l/s) continued through the flume system to the Childs plant. Large relict travertine structures alongside the modern channel (Fig. 3B) provide evidence that, for many kilometers downstream of the dam site, the pre-diversion stream morphology was dominated by deep pools formed behind several-meter-high travertine dams. After diversion of the baseflow, the in-channel travertine structures were breached and largely destroyed by episodic floods and debris flows. Active channel-spanning travertine dams survived only in a ~1 km reach downstream of the Irving power plant, supported by ~150 l/s return flow, and in a 500 m reach downstream of the diversion dam, supported by ~5 l/s seepage flow (Malusa et al., 2003).

The short reaches of active travertine provided refuge habitat for native fish, including five species federally-listed as endangered or threatened, which were badly affected by the virtually complete dewatering of Fossil Creek, as well as by the introduction of non-native species (Marks et al., 2006). Following a prolonged public campaign to restore Fossil Creek, the dam owner, Arizona Public Service agreed to decommission the entire hydroelectric project, and remove the dam (Marks, 2007). The diversion was shut down and full baseflow restored to the creek on June 18, 2005; the dam structure was removed in September 2008.

Prior to flow restoration, Malusa et al. (2003) took advantage of a temporary return of baseflow during a turbine maintenance event to estimate travertine precipitation rates from analysis of downstream changes in water chemistry and discharge. Malusa et al. (2003) calculated a precipitation rate of 12 Mg/day, over a distance of 6.7 km downstream of the springs, and found elevated deposition rates on artificial substrates placed on crests of existing travertine dams. These results, and accounts of rapid travertine growth rates in other travertine streams (e.g. Drysdale and Gillieson, 1997; Pentecost, 2005), led to the expectation that the travertine dams of Fossil Creek, and the threatened ecosystem they support, would rapidly return following flow restoration (Marks et al., 2006).

The emergence of travertine dams from the process of $CaCO_3$ precipitation is fundamentally a result of positive feedbacks. If travertine growth was uniformly distributed across the channel bed and banks, the channel morphology would remain largely unchanged as travertine accumulated; spatially uniform vertical growth would dominate. In Fossil Creek, following flow restoration we observed travertine precipitation on every surface within the active flow, however volumetric accrual of travertine has been much more rapid within dam complexes than in other morphologic units, such as pools and glides. How are the emergence, growth and long-term stability of travertine dams influenced by the interactions of abiotic physiochemical processes with living organisms?

3. Conceptual models of biotic–abiotic interactions

Here we consider three conceptual frameworks, where biotic factors: (1) independently modulate the rate of physical and chemical processes that produce travertine dams in a fundamentally abiotic feedback loop; (2) combine with abiotic factors in a set of mutually reinforcing feedback loops; and (3) work in opposition to abiotic processes, such that the travertine step-pool morphology reflects a dynamic balance between dominantly-biological constructive processes and dominantly-abiotic destructive processes. Each of these three frameworks is useful for understanding travertine streams, but is sufficiently general to be applied to other coupled ecogeomorphic systems.

3.1. Biotic influence on feedback between hydraulics and chemical precipitation

An abiotic feedback between flow hydraulics and travertine precipitation has long been recognized, in hot (thermogene) springs (30–45 °C) and cold (meteogene) springs (10–20 °C), such as Fossil Creek (Pentecost, 2005; Goldenfeld et al., 2006). This feedback can be cast in terms of two distinct mechanisms, the first a depth-averaged view (e.g. Hammer et al., 2007), the second focused on the boundary layer at the water–substrate interface (e.g. Liu and Dreybrodt, 1997). Where flow accelerates, for example where water surface slope

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Fig. 3. Photographs. A) Fossil Creek diversion dam (~8 m in height), B) relict pre-diversion travertine structure, C) travertine dam prior to trapping large woody debris (LWD), and D) same dam 1 year later with trapped LWD, E) channel-spanning travertine dam (crest ~50 cm above downstream water surface), F) algae trapped on dam crest (water flows left to right; photo foreground spans ~3 m), G) macrophytes (~5 cm in height) colonizing travertine dam surface, flow is from right to left, H) travertine eroded in winter flood from an actively forming dam, I) magnet housing tube exposed by erosion (protruding ~7 cm).

steepens approaching a freefall, the internal fluid pressure decreases as flow velocity and kinetic energy increase. With lower pressure, less CO_2 can be held in solution and the rate of CO_2 release to the atmosphere increases (Hoffer-French and Herman, 1989; Hammer et al., 2007). Lower dissolved CO_2 concentration results in higher degree of super-saturation of calcium and bicarbonate ions, and faster rates of travertine precipitation (Herman and Lorah, 1988).

At the scale of individual mineral crystals on the travertine surface, an important limitation to crystal growth is the rate of diffusion of dissolved ions across the thin laminar-flow 'sub-layer', from the turbulent flow, which serves as a reservoir of dissolved constituents. As the bulk flow becomes more turbulent, the laminar layer becomes thinner, the concentration gradient becomes steeper, and the flux of dissolved constituents to the boundary layer is increased (Liu and Dreybrodt, 1997). Travertine precipitation is, thus, enhanced at locations of increased turbulence (Lorah and Herman, 1988; Drysdale and Gillieson, 1997), and where travertine growth increases the local flow turbulence, such as flow over dams or other obstructions, a positive feedback results. This abiotic feedback loop is depicted in subpanel A of Fig. 4.

Living organisms modulate the rate of travertine deposition in many ways, and given the ubiquity of microbial life, travertine growth may rarely if ever be truly abiotic. The influence of biological processes can be conceptualized as simply increasing, or in rare cases decreasing, the efficiency of individual components of a fundamentally abiotic geochemical process, as depicted in subpanel B of Fig. 4. Living organisms contribute to the precipitation of $CaCO_3$ to form calcite crystals, and also to the volumetric accrual of travertine,

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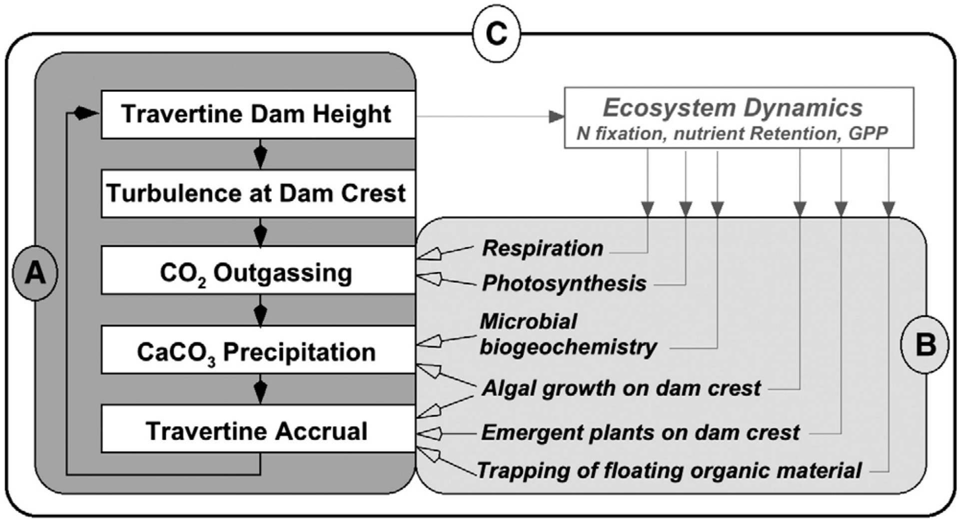

Fig. 4. Conceptual frameworks for interactions between biological and geomorphic processes in travertine growth. A) Abiotic positive feedback loop between flow hydraulics and geochemistry leading to growth of travertine dams. B) Set of individual biological processes that modulate abiotic physical and chemical processes. C) Nested feedback loops in which the strength of biological influences on travertine growth depends on ecosystem response to travertine morphology.

which in Fossil Creek is a porous composite of carbonate minerals, organic materials, and silicate sediments. In newly-formed travertine, the mineral component can be quite small, with the volume composed mostly of organic material and void space (Pentecost, 2005). Over time crystal growth fills in void space, and as organic material decomposes, mineral material replaces it, creating ‘fossils’. The supply of organic materials to the growing dam, through trapping of floating algal mats and leaf litter and the *in situ* growth of algae and macrophytes, thus influences the rate of travertine volumetric accrual; greater supply of biomass leads to faster dam growth all else equal. Many other biotic processes can be incorporated into the conceptual framework of the bio-mediated abiotic feedback depicted in Fig. 4, such as the effects of respiration and photosynthesis on dissolved CO_2, the role of microbes in controlling pH in the laminar boundary layer, and the role of trapped woody debris in providing a perturbation to the channel morphology that initiates the feedback between flow hydraulics and travertine deposition.

3.2. Feedbacks between travertine growth and ecosystem dynamics

Travertine step-pool morphology provides enhanced habitat for many living organisms, thus creating the potential for a primary role for biology in the feedback system that produces travertine dams. This has been demonstrated in Fossil Creek, where prior to flow restoration, Marks and colleagues (Marks et al., 2006; Carter and Marks, 2007; Compson et al., 2009) found striking differences in ecosystem dynamics between the travertine-dominated step-pool reach below the Irving power plant and riffle-pool reaches where travertine morphology was absent (Fig. 5). For example, gross primary productivity in travertine was double that of the non-travertine riffle-pool morphology, with algal growth in particular higher by a factor of five (Marks et al., 2006). Decomposition, measured at both the plot scale and respiration measured at reach scale was approximately three times greater in the travertine (Marks et al., 2006; Carter and Marks, 2007). Similarly, retention of leaves and key nutrients such as ammonium, was significantly elevated within the travertine reach (Compson et al., 2009; Gibson and Marks, unpublished data). These quantitative measures of ecosystem response to travertine are consistent with the strong qualitative impressions even a casual visitor might obtain: the travertine step-pools of Fossil Creek are hotspots of biological activity, compared to the reaches with non-travertine morphology downstream.

Recognition of the positive influence of travertine growth on ecosystem dynamics suggests conceptualizing the interaction of biotic and abiotic processes as a pair of nested feedback loops with numerous linkages, as illustrated by subpanel C in Fig. 4. Growth in the size of travertine dams can increase flow velocity and turbulence at the dam crest and plunge pool, and can also create improved habitat for microbial communities on dam crests, and for algal and macrophyte growth on dams and within the upstream pools. Increased population density and diversity, and faster rates of biomass production drive more efficient CO_2 outgassing, calcium carbonate precipitation, and travertine accrual through numerous mechanisms, including changes in water chemistry within the boundary layer, growth of autochthonous flora at the dam crest and trapping of allochthonous material carried by the flow from upstream.

Restoration of spring-fed baseflow following a century of nearly complete flow diversion has initiated a rapid transient evolution of the channel morphology that may include other positive feedbacks between geomorphic change and biological dynamics. For example, significant vegetation encroachment occurred during the near-absence of perennial flow. The base of trees established in the historic channel are now submerged by the restored baseflow, often in pools behind newly-formed travertine dams, and are likely to die from anoxic root conditions. As the riparian cover retreats, and solar insolation to the channel increases, algal growth may accelerate and contribute to faster travertine dam growth and further flooding of riparian vegetation; dead trees provide logs, branches and leaves that can be trapped at dam crests, promoting even faster travertine growth.

3.3. Erosion and the competition between biotic and abiotic processes

When positive feedbacks are particularly strong, a runaway cascade can occur, which in the case of biologically-driven travertine growth could provide an explanation for the formation of huge dam complexes and deep lakes such as at Plitvice, Croatia (Emeis et al., 1989). At Fossil Creek, however, abundant evidence exists that over long time scales (10^2–10^5 year) the creek is incising into bedrock. First, the widespread exposure of bedrock in the active channel bed, including durable basalt, indicates that whatever sustained travertine growth occurred prior to the flow diversion, erosion by flood flows over the past century has reset much of the valley floor to bare bedrock. Second, relict travertine structures can be found on terraces and hillslopes 10s and 100s of meters above the active channel (Feth

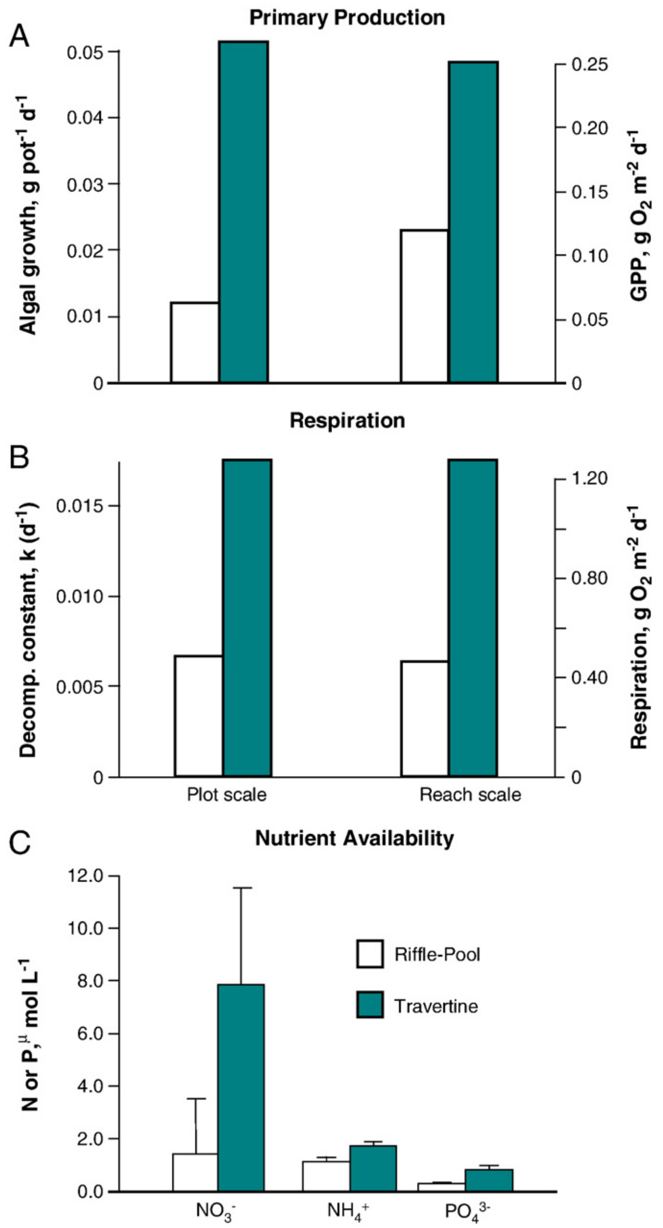

Fig. 5. Ecosystem response to travertine morphology. Compared to non-travertine riffle-pool morphology downstream on Fossil Creek, travertine dams enhance: A) primary productivity, B) respiration, and C) nutrient availability (modified from Marks et al., 2006; Carter and Marks, 2007).

and Hem, 1962; Malusa et al., 2003), indicating that prolonged net incision has occurred despite the opposing effect of travertine growth. Although large floods and boulder-laden debris flows are apparently capable of wiping out in-channel travertine structures and incising into underlying bedrock, travertine regrowth occurs so rapidly that it is reasonable to assume – neglecting recent human interference – that over time, travertine step-pool morphology dominates the channel except during brief, catastrophic disturbances.

The long-term average channel geomorphology can, thus, be viewed as resulting from a competition between the constructive effects of biologically-driven travertine growth and the destructive abiotic processes of erosion during floods. The magnitude and frequency of constructive versus destructive events are vastly different. Travertine growth occurs at the steady pace at which the baseflow delivers dissolved ions, and at which algae grows atop dam crests. Growth is also punctuated by the arrival and trapping of organic matter, from leaves to logs, and by the spring and fall blooms of algae, particularly the filamentous algae that grows in pools and collects on dam crests after the bloom has waned. In contrast, we hypothesize that floods with the power to significantly erode travertine occur on a time scale of 1 to 10 years, and those that reset the channel bed back to bedrock have recurrence intervals probably on the order of 10^2–10^3 years.

We can use the effective discharge concept (Wolman and Miller, 1960) to consider the interactions and potential feedbacks between constructive biotic and destructive abiotic processes. The effective discharge is the flow magnitude responsible for accomplishing the most net geomorphic work, given its frequency of occurrence. Where geomorphic work is defined simply as suspended or bedload sediment transport the most effective discharge is an event of moderate frequency and magnitude (Wolman and Miller, 1960; Andrews, 1980), because low magnitude flows transport little to no sediment, despite frequent occurrence, and high magnitude discharges occur too infrequently, despite high potential transport capacity. Because sediment transport is the dominant process that shapes the beds and banks of alluvial rivers, the effective sediment-transporting discharges commonly correlate with bank-full discharge, with recurrence intervals of ~2 years (Andrews, 1980; Emmett and Wolman, 2001).

In streams with travertine step-pool morphology, geomorphic work can be defined as the volumetric growth or erosion of travertine dams. We hypothesize that in Fossil Creek two distinct effective discharges occur: the constructive-phase baseflow during which most travertine growth occurs, and a characteristic rare destructive event capable of destroying travertine dams and reshaping the channel morphology. This is consistent with the analysis of Doyle et al. (2005), who applied the effective discharge concept to ecological processes in streams and found that the most commonly-occurring discharge (i.e. baseflow) can be the most ecologically effective for many processes, including the supply of nutrients and organic matter. Although biotic processes do not contribute directly to travertine erosion, the relative strength of biotic forcing of travertine growth could influence the magnitude of the effective erosional discharge. Where travertine growth rates are strongly enhanced by biotic effects, larger, more powerful floods would be required to reset the channel morphology; therefore, the magnitude of the effective erosional discharge may reflect the strength of positive feedbacks between travertine growth and ecosystem dynamics.

3.4. Testing for relative influence of biotic and abiotic processes

Guided by the three conceptual frameworks described above, we designed our field data collection to answer the fundamental question: what is the relative importance of biotic and abiotic processes in the morphodynamics of travertine growth and erosion in Fossil Creek? In particular, which mechanisms are responsible for the fastest growth rates, and how are those mechanisms distributed in space and time? Do we see evidence for purely abiotic feedbacks in dam formation and growth, or are biological processes important wherever feedbacks occur? What discharges are required for travertine to erode, and how widespread is erosion when it does occur? How do erosional events contribute to the long-term geomorphic evolution of the system? Is our hypothesis of a bimodal effective discharge regime supported? In the following sections we describe our field methods and results, divided into three parts following an idealized life cycle of a travertine dam: dam formation, growth, and erosion or abandonment.

4. Travertine dam formation

4.1. Overview of dam formation following flow restoration

Within months of the restoration of spring-fed baseflow in June 2005, hundreds of nascent travertine dams emerged from the channel bed, over a stretch of river extending more than 10 km downstream of the diversion dam. Dam formation was catalyzed by a wide variety of flow obstructions and perturbations, including pre-existing boulder and bedrock steps and woody debris pieces or accumulations. All of these settings share a common hydraulic attribute: localized flow acceleration and increased turbulence.

Several geomorphic settings correlate with emergence of travertine dams without clear biotic forcing, including: 1) channel constrictions, where flow accelerations and shorter cross-stream distances can facilitate channel-spanning dam formation; 2) bedrock steps, which are discussed in more detail in the following section; 3) on steeper slopes, from more rapid and possibly supercritical flow; and 4) where flow is roughened by emergent boulders, such that dams are created by travertine infilling of gaps between boulders. Dam formation appears to be suppressed in deeper pools and glides, which generally have lower slopes and flow velocity, and in some steep, narrow, smooth-walled bedrock slots where travertine deposits primarily in thin approximately uniform-thickness laminations, which we refer to hereafter as "plating".

Many dams were formed by flow perturbations caused by organic material, including: 1) LWD jams, where travertine fills in the gaps between branches; 2) single fallen trees, often oriented parallel to the main flow, creating initially isolated travertine deposits that later tend to merge with other LWD accumulations to form sinuous channel-spanning dams; 3) emergent plants that had colonized the lower elevations of the dewatered channel; and 4) accumulations of leaves, particularly in steep and wide reaches where flow is shallow. In many places the stream is multithreaded as it flows around islands formed by boulders stabilized by mature trees. Nascent dams were common in the higher elevation secondary channels that carried less flow, particularly in the steep descents approaching the confluence with the primary channel.

Our first major field campaign was mounted one year after the restoration of full baseflow. Overall, it was difficult to systematically determine the primary trigger for dam initiation because travertine deposition was so rapid that the channel substrate and basal or interior material of the dam were obscured by a continuous cover of travertine. The questions of what controls the location and spacing of travertine dams, and the dynamics of dam competition through submergence by more rapid growth of downstream dams, will be addressed in another manuscript. Here we focus on travertine deposition on bedrock steps, where we observe a pattern consistent with an abiotic positive feedback that will eventually lead to the emergence of channel-spanning dams. In this setting, we can ask whether the dynamics are truly abiotic (Fig. 4A) or whether living organisms play either a supporting (Fig. 4B) or essential (Fig. 4C) role in this type of travertine dam formation.

4.2. Dynamics leading to dam emergence on bedrock steps

Bedrock steps are a common feature along the study reach. Sub-vertical drops of 1–3 m are formed primarily in basalt, which is jointed at the meter scale and appears to erode by detachment of large blocks. Reaches lacking bedrock steps are typically underlain by ash layers in the volcanic valley-bottom fill, or have large accumulations of boulders that are delivered by steep tributaries or landslides (Fuller, 2009). A striking feature of large bedrock steps in Fossil Creek is the presence of large relict travertine structures on terrace surfaces adjacent to the active channel. The relict travertine dams commonly align parallel to the active step, and suggest that a large channel-spanning travertine dam existed on top of the step prior to flow diversion a century ago (Fig. 6A). The exposed base of the relict structures adjacent to the channel shows layers of thin travertine laminations, overlain by the more massive and irregular travertine deposited in association with accumulations of organic material (Pentecost, 2005). We observe widespread travertine plating on the upper lip of the bedrock steps, which we interpret as evidence that travertine dams will reform in these same locations, because of the hydraulic forcing of the flow over the bedrock step.

4.2.1. Measuring travertine accrual and flow depth

We chose a prominent bedrock step located 3.7 km downstream of the diversion dam for detailed analysis. We hypothesized that travertine plating thickness would be non-uniform across the step, and would correlate with flow velocity. To measure the thickness of travertine accumulation since flow restoration we used a rotary hammer with a long extension bit to drill holes through the travertine, stopping immediately when we hit the much harder underlying basalt (Fig. 6B). To quantify the effect of variable flow velocity without making direct velocity measurements, we chose transects oriented parallel to the flow, where we could be confident from the lack of lateral slopes of the bed and water surfaces that the flow was neither divergent nor convergent. The absence of a significant lateral velocity component along the transects allowed us to assume that discharge per unit width (q) was constant along the transect. We then used measurements of variable flow depth (h), as a proxy for differences in mean flow velocity (u), with the conservation of mass relation $uh = q$. We used a total station to survey the locations of the holes, which were spaced 10 cm apart, and the topography of the travertine surface. We used a micrometer to measure travertine thickness to the nearest 0.5 mm, and a stadia rod or ruler to measure the mean flow depth, with a precision of <5 mm. We are confident from accounts of the channel conditions at this location that the bedrock surface at the lip of the step was devoid of travertine, presumably because of frequent scour by bedload transported in flood flows.

4.2.2. Spatial variation in travertine accrual

Fig. 7 shows profiles of bedrock, travertine and water surface elevation for two transects, for measurements made in June 2008, three years after restoration of baseflow. Both transects show decreasing water depth as the flow accelerates toward the lip and much thinner flow across the steep upper face of the step. Travertine accumulation is negligible upstream, but thickens rapidly as the flow spills over the step lip. Note that we limited the length of the transect to avoid sampling under the hydraulic jumps and other turbulent structures on the lower portions of the step (Fig. 7A). Fig. 7C shows that travertine thickness is inversely correlated with flow depth, consistent with the expected pattern of variation in $CaCO_3$ precipitation rate with mean flow velocity that underlies the abiotic feedback described in the previous section. The 2008 data are well-fit by a power equation with an exponent of 2.1, and imply a strongly non-linear dependence of travertine growth on mean velocity.

Also plotted in Fig. 7C are measurements made in 2006 at a location 0.5 km downstream, which show a similar pattern, but with a significantly lower slope (0.5) in the log–log linear regression of travertine growth with flow depth. These measurements were made in a steep bedrock reach just above two large (>3 m) bedrock steps, at a location where the flow spills over a series of smooth undulations in the underlying bedrock, creating alternating zones of fast-shallow and slow-deep flow. Again, we were careful to select transects with no apparent flow divergence or convergence. Travertine thickness was estimated here by measuring with a micrometer the depths of narrow trenches cut into the weak travertine with a sharp chisel sliding along the hard basalt substrate. The differences between the 2006 and 2008 data can be attributed to several factors, including: two additional years of travertine deposition in 2008, which accounts for the higher maximum accumulation in the fast-shallow flow; the deeper locations in the 2006 survey were in the middle of a steep reach where CO_2 outgassing in fast flow immediately upstream may have initiated $CaCO_3$ precipitation that extended into slower moving water downstream; and the possibility of differential erosion of the upstream portion of the step measured in 2008, by bedload material

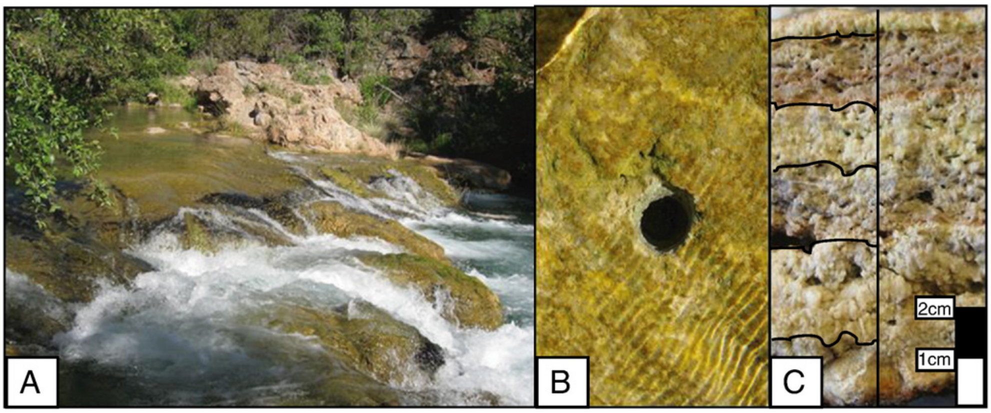

Fig. 6. Travertine deposition on bedrock step. A) Flow over bedrock step face where transects of erosion holes were drilled; note relict travertine structure on left bank aligned with step; B) 15 mm diam. hole drilled in active travertine to measure depth of accrual; C) vertical profile of travertine sample showing banding indicative of variable algal contribution to travertine accrual; darker bands correspond to elevated organic content.

that moved in suspension through the much steeper downstream segment.

4.2.3. Inferring potential for dam emergence

We interpret the overall pattern of focused travertine deposition as evidence of the potential for emergence of a travertine dam from the interaction of flow hydraulics and bed topography. Projecting forward in time, continued growth of travertine at the upstream lip above the steep face of the bedrock step will exaggerate the existing differences in hydraulics upstream and downstream of the lip, and reinforce the tendency for travertine growth to occur at the flow lip. Downstream of the lip, a broad zone of convergent and divergent turbulent flow also has significant travertine deposition, with prominent algal mats particularly at points of flow divergence where water depth is low. The ~4 m length of the zone of deposition measured parallel to the flow, from the step lip downstream to the pool below, is similar to the width of the relict travertine structure on the adjacent left bank (Fig. 6A), suggesting that we have documented the earliest stages of the reformation of a travertine dam morphology closely resembling what existed here prior to the diversion dam construction. At the downstream site measured in 2006, continued focused deposition at the high points along the bedrock undulations should lead to emergence of a series of closely-spaced dams, similar to clusters of pre-existing travertine dams located immediately downstream of the Irving power plant.

4.3. Biotic contribution to bedrock step travertine accrual

Algae contributes to the volumetric accrual of travertine in the highly turbulent downstream portions of the step. Could algal growth and other biotic processes contribute to travertine growth more widely across the bedrock step, and play a significant role in this setting where the abiotic positive feedback is most clearly expressed? To answer this question we collected travertine samples from four distinct hydraulic settings in the bedrock step, including: the 'spillway' where the holes were drilled; a high 'ridge' location in the downstream turbulent step face, a 'fringe' deposit formed at the water surface on a vertical rock wall just downstream of the step lip, and a 'wall' deposit taken from a point several meters upstream of the lip, 30 cm below the water surface along a upstream-oriented vertical face. Each ~100 × 100 cm square sample was collected by scraping a trench down to the underlying basalt with a chisel around the perimeter of the sample, and carefully prying off the complete thickness of travertine using a sharp knife to detach the lowest layer from the bedrock.

In cross-section (Fig. 6C), the samples revealed that the travertine is composed of alternating dark and light colored layers, where the dark layers were similar in appearance to the algae-rich surfaces where active travertine deposition was taking place. We measured the percent organic content of both the bulk samples and representative dark and light colored layers using the Ash Free Dry Mass (AFDM) method, described in detail in Marks et al. (2006). From the four samples we tested a total of 11 layers, 4 light and 7 dark colored, with 5 replicates from each layer and bulk sample, for a total of 75 AFDM measurements. To compare layers, and remove the confounding effect of sample location, we normalized each replicate by the mean of the bulk sample. A '*t*-test' shows that the dark layers are significantly ($p = 0.03$) elevated in organic content, and confirms our hypothesis that the dark color indicates a higher percentage of algal material. The thickness of the layers was highly variable, both within and between samples, however, the dark layers were the dominant component of each sample. For the 'spillway' sample, which is representative of the environment where we measured the variation of travertine thickness with flow depth, the dark layers composed roughly 80% of the overall thickness of the travertine accrual, although the organic content was slightly lower in the light and dark layers compared to the samples taken from other locations.

We conclude that the biological contribution to travertine accrual is important, even in deposition of thin laminations at flow accelerations across the lip of bedrock steps. Moreover, the color banding of the travertine suggests that plating growth is most rapid during the seasonal algal blooms. Because the travertine deposition in the bedrock step setting is perhaps the best expression of the putative abiotic positive feedback between flow hydraulics and travertine growth, these results suggest that biologically important factors such as nutrient availability, solar insolation, and species composition, should be considered in modeling travertine morphodynamics, even in this environment. Because the elevated locations of rapid travertine growth on the bedrock steps have not yet grown sufficiently to affect the upstream channel conditions, no evidence exists in this location of a positive feedback between travertine growth and habitat quality, as depicted in Fig. 4C. The role of algae in modulating travertine accrual is consistent, however, with the conceptual model in which biology is an important and independent factor in the otherwise abiotic geomorphic dynamics (Fig. 4B).

5. Travertine dam growth

5.1. Overview of travertine dam growth

Spatial and temporal differences in the rate of vertical accrual of travertine dams will control the long-term evolution of the channel morphology in Fossil Creek. For example, the scaling of dam spacing and pool size will depend on relative growth rates of adjacent dams

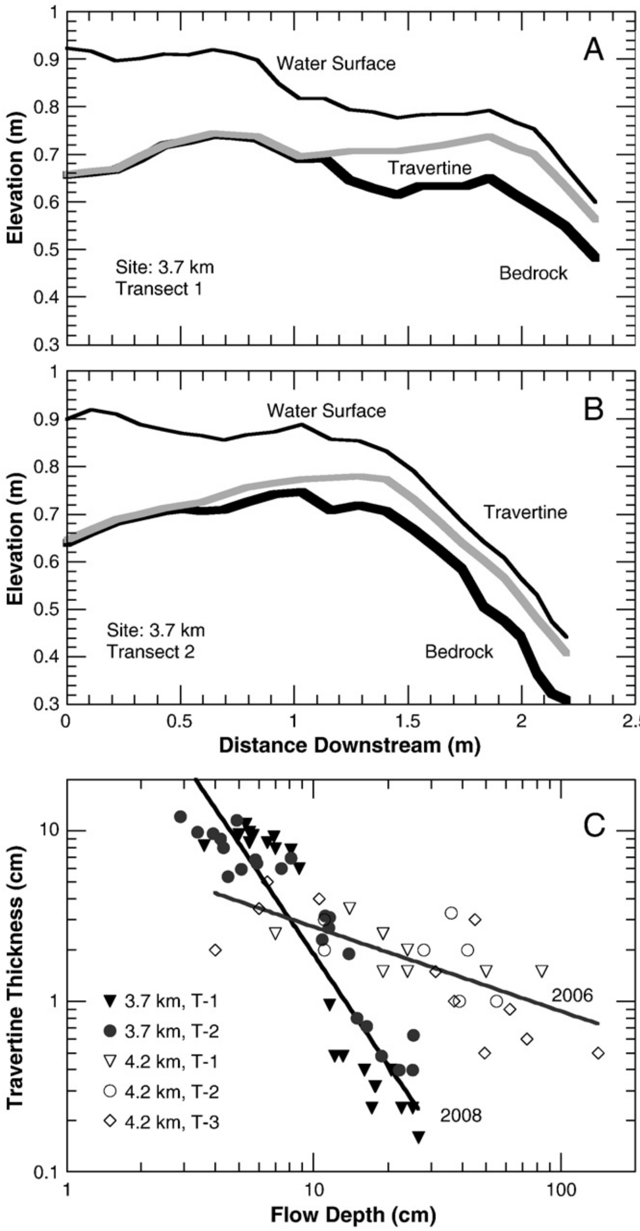

Fig. 7. Variation in travertine accrual with flow depth on bedrock steps. A and B) longitudinal profiles of bedrock, travertine and water surfaces at top of bedrock step shown in Fig. 6A, for transects 1 and 2 respectively. C) Negative correlation between flow depth and travertine thickness; measurements made in 2008 along two transects shown in panels A and B, and three transects measured in 2006 at a bedrock step at station 4.2 km downstream of the diversion dam.

within a reach (Goldenfeld et al., 2006). Dams that grow more rapidly may submerge upstream dams, and suppress the factors such as flow acceleration and trapping capacity that drive dam growth. Similarly, rapidly growing dams are more likely to escape submergence by pools formed behind dams immediately downstream. Moreover, rapid initial dam growth increases the probability that sufficiently-deep upstream pools, which limit the erosional effectiveness of episodic floods, are formed before a large flood occurs. Here we explore the relative influence of biotic and abiotic factors on the magnitude and rate of growth of travertine dams, including dams formed after the restoration of baseflow in June 2005 and the pre-existing dams below the diversion dam and the Irving power plant.

Factors influencing travertine growth vary over many length and time scales. Mineral precipitation occurs at the scale of individual crystals ($\sim 10^{-6}$ m), while the supply of dissolved ions available for crystallization varies with distance downstream of the spring source ($\sim 10^3$ m). Here we consider three scales at which we have sought to distinguish and characterize the abiotic and biotic factors that control travertine dam growth rates. The first is the scale of the long profile, over which the supply of chemical constituents varies, as do other factors such as the watershed drainage area that generates erosive floods. The second scale encompasses a reach (~10 channel widths), where we find sequences of dams developed, for example on a mean local slope. The third scale is the decimeter length scale at which we can measure travertine dam growth, characterize local conditions and materials, and test hypotheses for what controls differences in growth rates across this and all larger scales.

5.2. Measuring dam growth and erosion

We selected 18 reaches for detailed study, spaced roughly equally along the 10 km length of the study area, identified by station in km downstream of the diversion dam (Fig. 2C). Within each reach we used a total station to survey the locations and elevations of travertine dams, and to characterize the mean channel width and (in most locations) the bed and water surface slope. We established benchmarks and repeat photo points, and used GPS to georeference the benchmark locations. For each location we also made detailed sketch maps, recording attributes such as local flow orientation, and the position of boulders, large trees and relict travertine structures. After processing the survey data we redrew the sketch maps on base maps scaled by the benchmarks and other surveyed points.

To measure the change over time in the elevation of specific points along travertine dams, we developed a new micro-topographic surveying technique based on measuring the magnetic field produced by small magnets, which we embedded within the travertine dams. To keep the magnetic field axis oriented vertically, we glued the 0.5 cm thick, 1 cm diameter magnets into the base of 10 cm long pvc tubes, which were installed into holes drilled in the crests of travertine dams. As depicted in Fig. 8, the magnetic field intensity decreases geometrically with increasing distance. We use a Schoenstedt GA-72Cd magnetometer, which is sensitive to <1 mG, placed on the dam surface directly above the magnet, to measure the local field intensity (Figs. 3C and 8). The measured value is derived from the gradient in field intensity along the length of the magnetometer (Earth's magnetic field is approximately uniform at this scale). Using a calibration curve (Fig. 9) developed from measurements at known depths within travertine of various compositions, we convert a measurement of magnetic field intensity to an estimate of depth to the magnet. Changes in field intensity over time can then be converted into estimates of travertine growth or erosion.

Estimates of depth-to-magnet made when the magnet location is unambiguous are precise to within 0.5 mm at a 95% confidence level. Uncertainty in estimated growth can be considerably larger, and increases with growth, because as the crest morphology of the travertine dam evolves, the exact location of the magnet becomes

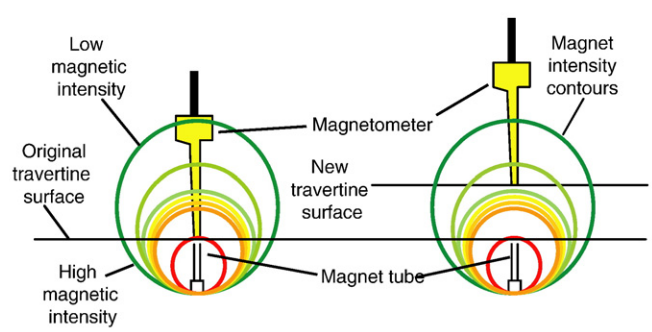

Fig. 8. Magnet method for measuring vertical accrual of travertine. Schematic illustrating how the decrease in magnetic intensity with distance can be used to measure changes in travertine thickness.

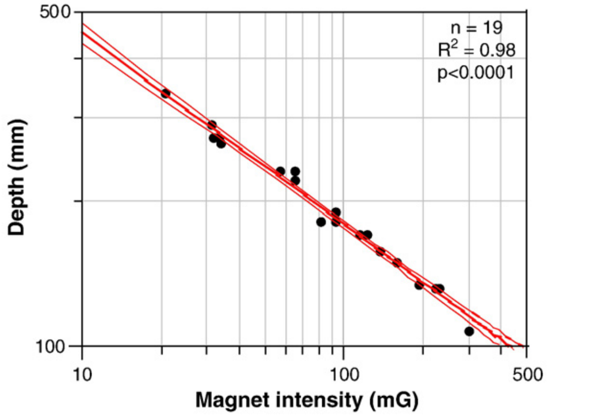

Fig. 9. Calibration curve used to estimate depth of magnet from measured magnetic field intensity. Data from calibration magnets installed at known depths.

more difficult to determine. The full method, including a detailed analysis of the sources and propagation of uncertainty was developed as part of the first-author's MS thesis (Fuller, 2009), and will be described in a separate manuscript. Here we report growth and erosion estimates categorized by whether the absolute elevation difference is greater or less than the least significant difference (LSD), calculated for a 90% confidence level.

We have installed a total of 252 magnets in 94 dams, distributed non-uniformly across the 18 sites within the study area. Between June 2006 and July 2008 we made frequent visits to Fossil Creek, and recorded 611 paired readings from which we estimate growth and erosion rates. When the magnitude of erosion exceeded the thickness of post-magnet-installation travertine growth, we estimated the vertical change using the length of the exposed PVC tube (Fig. 3I); when the magnet was completely removed by erosion we know that erosion magnitude must have been greater than the 10 cm length of the missing tube.

The time line of magnet installation and reoccupation measurements is depicted by the Gantt chart shown in Fig. 10, in which the number of magnets installed at each site is indicated by the vertical thickness of the band associated with each site. Depending on the time sequence of magnet installation and reoccupation, the number of individual magnet growth measurements at a given site varies from 1 to 5; each subsequent measurement interval is indicated Fig. 10 by increasing darkness of the shading.

Each magnet location was also surveyed by total station, making it possible to combine spatial and temporal data on the evolution of travertine dam crest elevations within a site. Fig. 11 shows maps of dam, magnet and channel bank locations for the 130 m reach just below the diversion dam (Station 0.1). The upper and lower maps show measurements of vertical change at each magnet location of the periods June 2006–June 2007 and June 2007–July 2008 respectively. To provide a visual impression of the distribution of growth and erosion, the data are grouped into five categories, depending on whether growth or erosion occurred, and whether the absolute magnitude of change was greater or less than 100 mm or the LSD. The results indicated in Fig. 11 will be discussed in more detail below.

5.3. Growth rates of travertine dams

An inherent tradeoff exists between precision and temporal detail in analyzing the data obtained from the repeat magnet measurements. If we use the shortest-period measurements, we obtain the largest data set, but also the greatest number that are not significantly different from zero (i.e. less than the absolute value of the LSD). The distribution of the growth rates (including erosion, for which 'growth' is negative) measured over the shortest period for each magnet is shown in Fig. 12A. Growth rates and erosion rates are approximately log-normally distributed, so for clarity of presentation we have used a log-transformed horizontal axis and define negative growth as positive erosion. The 611 total data points include 409 growth rates (143 are significant) and 202 erosion rates (104 are significant). In the data analysis reported below, we treat the two types of change separately, considering growth rates first, and defer further discussion of erosion rates until the following section.

To minimize the uncertainty in our overall conclusions about biotic and abiotic controls on the growth rates of travertine dams, we chose

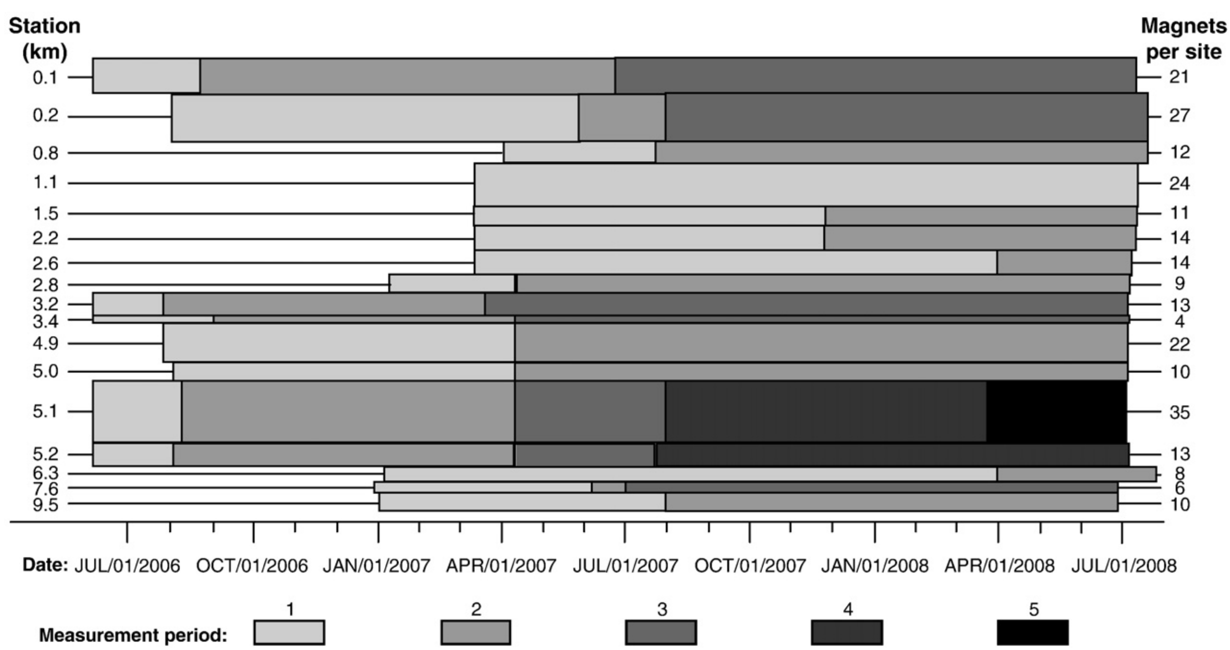

Fig. 10. Gantt chart showing time sequence of measurements for each magnet site. Thickness of each horizontal bar corresponds to number of magnets installed at each site (listed on right). Shading indicates sequence of measurement intervals; the lightest shade is the first site-specific measurement interval and subsequent measurement periods increase in darkness. Rate of topographic change was calculated as difference in measured elevation divided by length of time interval encompassed within shaded bar segment. Sites 9.4 and 9.6 from Fig. 2C are grouped and labeled as 9.5 here because of the small number of magnets deployed.

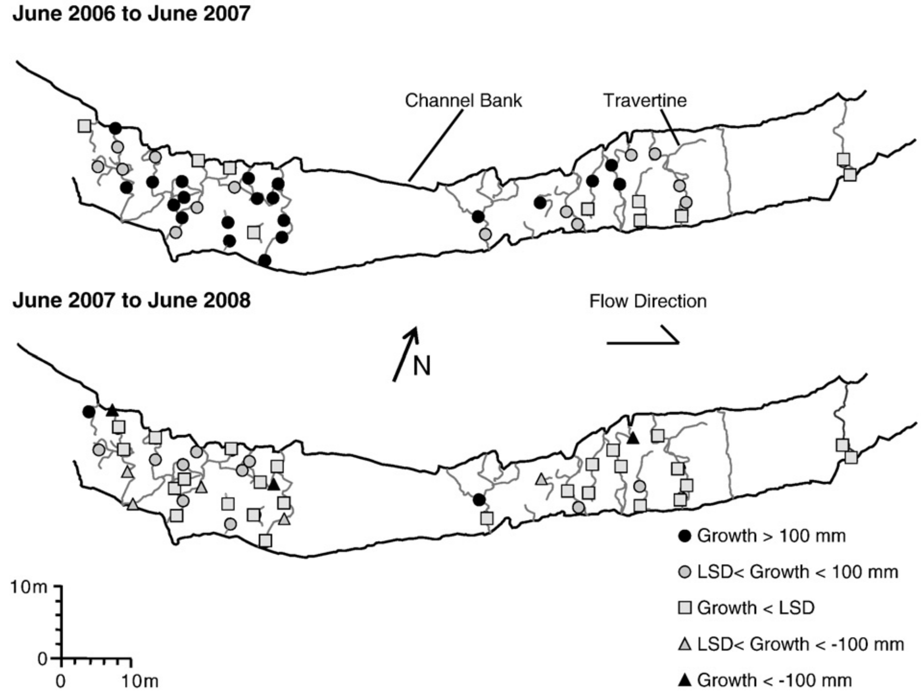

Fig. 11. Map of travertine dams and magnet locations for sites 0.1 and 0.2 km downstream from the diversion dam, for periods 2006–2007 and 2007–2008. Each magnet location is indicated by: a circle representing growth, a triangle representing erosion, or a square signifying that the change in travertine elevation was below the least significant difference calculated at the 90% confidence interval.

to analyze growth rates calculated over the longest period, which for the majority of magnets showing net growth encompasses the full two-year period of data collection. The distribution of the 165 longest-period growth-rate measurements is shown in Fig. 12B, where growth rates less than the LSD are indicated by dark shading. The average growth rate of all magnets showing net positive growth over the study period was 43 ± 4 mm/year (mean $\pm$ standard error); the median growth rate was 25.5 mm/year.

5.4. Reach-scale variation in growth rates

Fig. 12C shows growth rates plotted as function of distance downstream of the diversion dam, for the 165 magnets with net growth. A clear downstream decrease occurs in net growth rate, which we fit with an exponential function. Also evident in Fig. 12C is the tremendous within-site variability, which in part reflects differences in local conditions at the scale of individual dams and magnet sites. The apparent effect of station on log-transformed growth rates explains only 26% of this variability. Of the many possible sources of the downstream decrease in growth rates, the reduction in available dissolved ions from upstream travertine deposition is the most obvious (Malusa et al., 2003). Other possible explanations include systematic downstream variation in growth-promoting biotic factors, or a gradient in the contribution of small magnitude erosion that limits the size of net growth calculated over this longest time interval.

To investigate sources of inter-site variability, we calculated the mean of the log-transformed growth rates for each site, which are plotted against station in Fig. 12D. For this calculation we subdivided sites with significant intra-site slope variations, and excluded sites where we had only three or fewer magnets. An exponential fit to the site-mean growth rate explains 64% of the inter-site variability. Although overall channel slope does not change significantly through the 10 km study reach, the variation in local channel slope is negatively correlated with distance downstream (station). Regressing site-mean growth rate against slope does not show a significant relationship ($p = 0.12$), however, in a multiple linear regression, slope and station together explain 82% of the variation in site-mean log-transformed growth rate ($p < 0.1$). This suggests that the upstream length over which travertine deposition occurs and local channel slope are the dominant controls on the inter-site variations in average growth rates.

5.5. Inferring biotic and abiotic growth mechanisms at the small scale

We hypothesize that four dominant growth mechanisms occur at the decimeter scale: the primarily abiotic hydraulic process described above, hereafter referred to as 'precipitation', and three distinct biotic mechanisms. The first biotic mechanism is algal growth directly on the surface of the dam, which provides surface area for crystal growth, volumetric structure for travertine accrual, and habitat for micro-organisms that can influence boundary layer chemistry. Growth of emergent macrophytes on dam surfaces provides a second mechanism for travertine accrual because, in addition to sharing the same characteristics of algal mats, emergent plants are efficient at filtering floating organic matter, but also reduce water flow-through because of high roughness. The third mechanism is the trapping of floating organic material carried by the flow from upstream, including leaves, branches and other litter, logs, and algae such as the filamentous algae that blooms seasonally in the deeper pools. Trapping at dam crests is distinct from filtering by emergent plants because of the different hydraulic conditions at the dam crest. We henceforth refer to these three biotic mechanisms as 'algae', 'plant', and 'trapping'. The algae and trapping mechanisms can be also be classified as incorporating autochthonous- and allochthonous-organic material respectively, while the plant mechanism is a combination of the two.

To test for the occurrence and significance of these four mechanisms, we collected a large set of measurements of local attributes representative of conditions at the scale of individual magnets (Fuller, 2009). Each attribute was chosen to test a specific hypothesis for how that attribute can affect travertine growth, within the classification scheme of the four mechanisms defined above. For example, we measured water depth above each magnet at the time of reading each magnet. We hypothesize that precipitation rate should

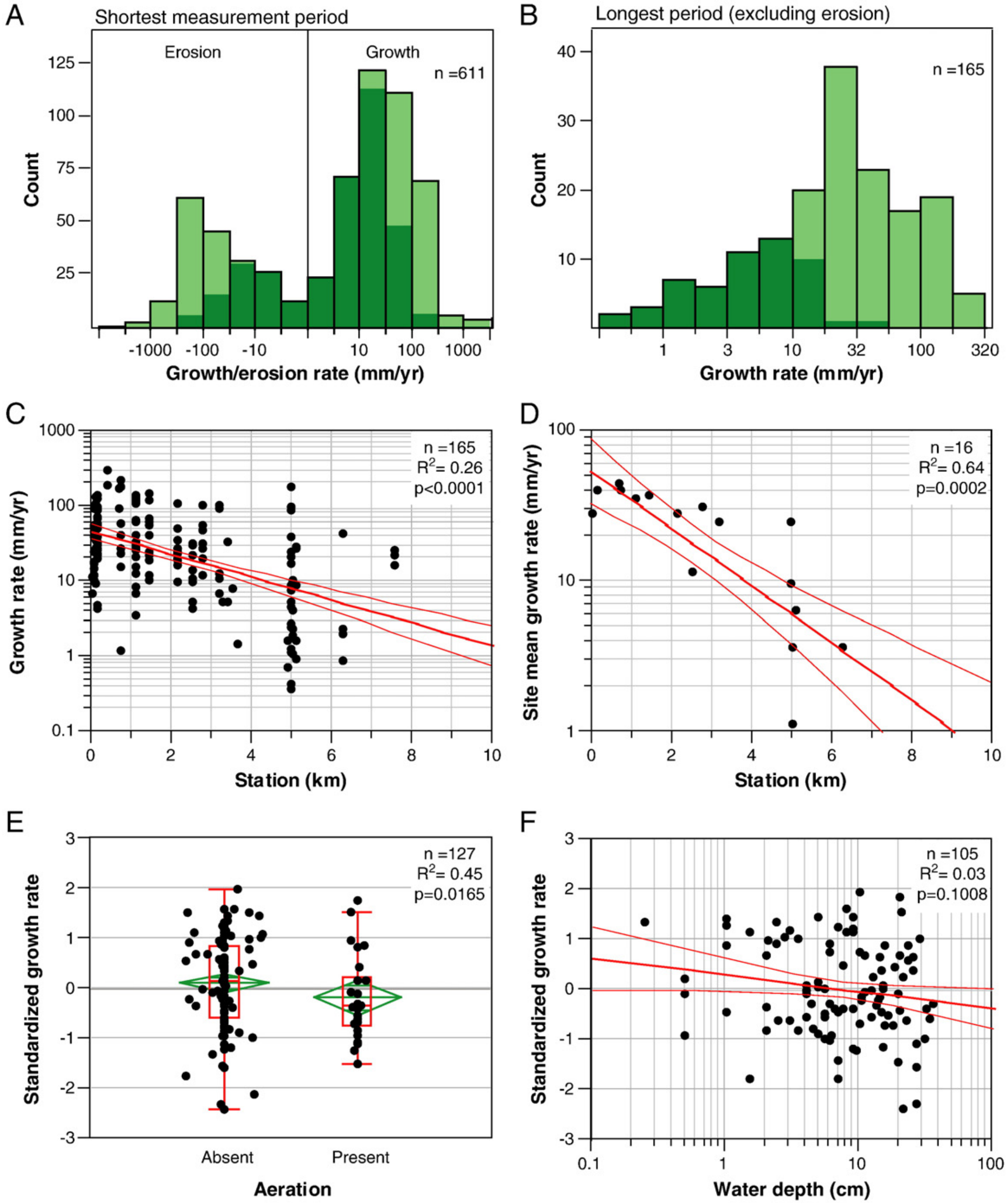

Fig. 12. Travertine dam growth-rate analysis. A) Distribution of all non-redundant growth-rate measurements with $\log_{10}$ binning, $n = 611$; light shading indicates statistically significant shortest-period growth rates at 90% level. The two inner-most bins encompass growth rates between −3.16 and 3.16. B) Distribution of the longest-period growth rate measurement for each magnet with $\log_{10}$ binning, excluding all negative values (erosion) $n = 165$; light shading indicates statistically significant growth. C) Growth rate as a function of station, excluding all erosion values. D) Site-mean growth rate as a function of station, excluding all sites with 3 or fewer growth measurements. E) *t*-test comparing $\log_{10}$ growth rate, standardized by site mean, as a function of presence and absence of flow aeration. F) Log_{10} growth rate, standardized by site mean, as a function of $\log_{10}$ water depth over magnet at baseflow.

be positively correlated with water depth because deeper flow will have greater mean velocity and higher potential flux of dissolved ions to the boundary layer. (This is different from the bedrock step analysis where we assumed constant discharge along a downstream-oriented transect; here we are comparing flow at different positions along a cross-stream-oriented dam crest, where discharge is generally not constant).

Hydraulic attributes we associated with the precipitation mechanism included: flow aeration (the presence of bubbles indicating high turbulence immediately upstream), upstream water surface slope (coded as flat or not-flat to identify shallow water depth locations with negligible active flow), and presence or absence of critical flow (estimated from the water surface response to perturbation). We also measured two topographic attributes: relief (largest elevation difference with a 10 cm radius of the magnet location) and whether the magnet was slightly upstream, downstream or exactly at crest of the dam surface. A key attribute that we used to identify dominant mechanism is the composition of the travertine dam surface, apparent from visual inspection without disturbing the dam surface. We used an ordinal classification scheme (absent, present and significant) for each of the following dam surface materials: mineral precipitate (dominantly calcite), algae, leaves, wood, and (non-algae) plants. Finally, to quantify the organic content of the travertine at the magnet location we used the AFDM method (Marks et al., 2006) to analyze samples collected from the dam surface. We collected samples by scraping a 5×5 cm area with a toothbrush at a point 10 cm from the magnet (to avoid eroding the location of the growth measurement), with the same water depth and apparent composition.

5.6. Hydraulic controls on travertine growth rates

The high within-site variability, shown in Fig. 12C, suggests that much information useful for understanding controls on travertine growth remains to be extracted from these data. To estimate the relative importance of the hypothesized biotic and abiotic mechanisms we next analyze individual magnet growth rates standardized as the local deviation from the site mean divided by the site standard deviation. Of the hydraulic and topographic attributes we documented, only two showed a statistically significant influence on standardized growth rates (90% confidence). Flow aeration was associated with lower growth rates, as shown by the *t*-test plotted in Fig. 12E ($p=0.017$). Similarly, standardized growth rates declined with increasing water depth, as shown by the fit line plotted in Fig. 12F ($p=0.10$).

Both of these relatively weak signals are opposite to what we originally hypothesized, however, both results might be interpreted as indirect evidence for strong biological influence on measured growth rates. The deeper and more aerated the flow, the less light can pass through the water column to reach submerged algal mats growing on the dam crest. Could these two attributes be unintended proxies for the algal growth mechanism? We can ask the same question of the downstream decline in growth rates shown in Fig. 12C. If dominantly-biotic mechanisms are primarily responsible for upstream travertine deposition, then the decline in available dissolved constituents could be viewed as a biologically-driven outcome. We next consider the role of biotic factors in explaining variations in growth rates at the inter- and intra-site scales.

5.7. Evidence for biological controls on travertine growth

The extent to which organic material is incorporated into the travertine dam surface, as quantified by the AFDM measurements, is a compelling indicator of variations in the strength of biotic influence on travertine dam growth. Fig. 13A shows the downstream variation in organic mass percent, with the data grouped by site in sequence from upstream to downstream. Analysis of variance (ANOVA) confirms that the grouping by site is highly significant ($p<0.0001$). Organic content is notably low at the two sites immediately downstream of the diversion dam, but increases rapidly downstream, reaching peak values at the sites within the second kilometer downstream. After declining through the third kilometer, organic content varies around a moderate mean value in the sites further downstream. With the exception of the sites in the first 0.2 km below the diversion dam, the downstream variation in organic content roughly matches the downstream trend in travertine growth rates (Fig. 12C).

To directly test the influence of organic content on growth rates, we fit a power relation to the data, and find a positive correlation as shown in Fig. 13B. Although organic content can only explain 7% of the total variability in travertine growth rates, we are confident at the 99.7% level ($p=0.003$) that the effect is real. The AFDM measurements most likely record the extent of algal growth at the dam surface at the time of sample collection. Algae are nearly ubiquitous on the travertine of Fossil Creek; we only recorded 18 locations where algae were absent, at the other 147 locations algae were categorized as either present (115) or significant (32). We can use the organic content data to test whether our algae attribute determinations reliably reflect meaningful differences in algal density. Fig. 13C shows the results of a *t*-test, which demonstrates that our qualitative assessment of significant algae growth is also a highly statistically significant predictor of high organic content in the surface travertine. This result provides quantitative support for the use of the ordinal-scale mechanism classification scheme, which we discuss next.

To estimate the dominant travertine growth mechanism at the magnet scale, we used the measurements of dam surface composition to group the growth rates according to the following scheme. Where algae was the only composition attribute rated 'significant' (all others absent or present), we assigned the magnet to the 'algae' mechanism group. Similarly, where 'calcite' or 'plants' were the only 'significant' attributes, those magnets were assigned to 'precipitation' or 'plants' respectively; magnets with significant 'leaf' or 'wood' (or both) were assigned to the 'trap' mechanism. Where magnets were classified as significant in calcite and in organic material, we assigned them to biotic mechanism associated with that material, reasoning that mineral precipitation is an essential part of every mechanism, and the biotic mechanisms are hypothesized to accelerate precipitation. All other magnets were deemed to have an indeterminate dominant mechanism and were excluded from the analysis.

Fig. 13D shows log-transformed travertine growth rates grouped by dominant mechanism, and analyzed by ANOVA. The differences among the groups are significant at the 94% confidence level. The fastest growth rates are associated with the emergent plant filtering mechanism, followed in descending order by the trapping and *in situ* algae growth mechanisms. Most importantly, the precipitation mechanism, which reflects an apparent lack of significant biological material at the travertine dam surface, is associated with the slowest growth rates. We interpret this trend as evidence for the importance of organic material in accelerating travertine growth rates, particularly allochthonous materials, which contribute to the two mechanisms associated with the most rapid growth rates. If we combine the three biotic mechanisms, a *t*-test shows that mean growth rates are significantly elevated (roughly double) for the biotic versus the abiotic mechanism, with 98% confidence (Fig. 13E).

In the preceding analysis we have not attempted to remove the effect of site-to-site variations, but rather have considered all sites at once, under the assumption that the differences in mean growth rates between sites (Fig. 12D) could in part reflect spatial variation in the strength of biotic influence. To explore the downstream variation in dominant growth mechanism, we plot, in Fig. 13F, the results of a logistic regression of mechanism against distance downstream of the diversion dam (station). This analysis suggests that the role of precipitation is fairly uniform along the length of the study area, but that a monotonic shift occurs in the type of biotic mechanism, from plant and algae growth upstream to trapping downstream.

5.8. Summary of growth rate results

To summarize the results reported in this section, we find: (1) rapid growth of travertine dams established (or rejuvenated) following flow restoration, averaging more than 2 cm/year, with many locations showing greater than 10 cm/year sustained over the two-year study period; (2) growth rates decline systematically downstream, consistent with a progressive loss of dissolved constituents because of upstream travertine deposition, but also broadly parallel to a decline in organic content in dam surface material and a downstream shift in dominant biotic mechanism; (3) at the length scale of individual measurements of magnet growth rates, the biotic mechanisms are strongly associated with the faster growth rates, and correlations between individual hydraulic attributes and growth rates are more consistent with biotic than abiotic controls; (4) growth rate measurements show tremendous spatial variability across scales, a finding that can be interpreted as characteristic of biological systems (Levin, 1992; Powell, 1995). We conclude that the multiple lines of evidence for a

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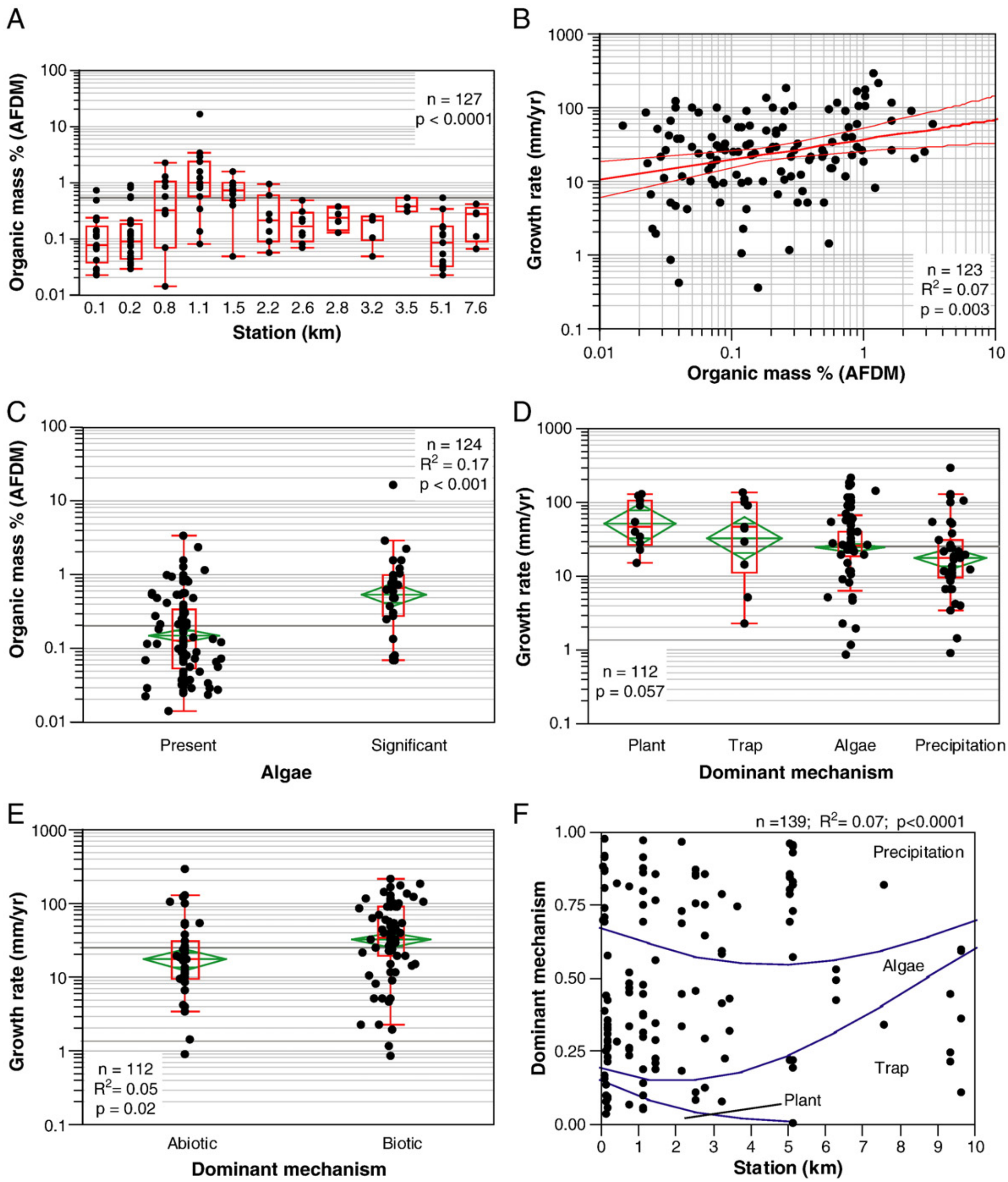

Fig. 13. Biological influences on travertine growth rates. A) Percent organic content (AFDM) in travertine dam surface at each site. B) Increase in growth rate with increasing percent organics, with 90% confidence curves. C) *t*-test showing significant difference in organic content (AFDM) with categorical estimate of algal abundance. D) ANOVA of travertine growth rates for each hypothesized mechanism. E) *t*-test showing significant difference in growth rates between magnet locations dominated by precipitation and all other growth mechanisms. F) Logistic regression of hypothesized mechanisms as a function of station.

strong influence of living organisms on rates of travertine growth, coupled with previously published evidence for the beneficial effects of travertine on ecosystem dynamics, demonstrate a positive feedback between biology and geomorphology as conceptualized in Fig. 4C.

6. Erosion and abandonment of travertine dams

Here we explore the temporal and spatial distribution of erosion of travertine during the two-year study period. We were fortunate to observe erosive flood flows in the summer monsoon season of 2007, and in the subsequent winter, when several rain-on-snow events caused widespread removal of travertine and channel avulsion at one site. In this section we address the following questions: (1) Is the pattern of erosion through time consistent with the bimodal magnitude–frequency framework proposed above? (2) Does the spatial distribution of travertine erosion help explain the downstream decrease in net growth rates, which we have previously considered in terms of abiotic and biotic controls on growth? (3) Do feedbacks exist between biotic and the abiotic erosional processes? (4) Does a morphodynamic signature of life emerge from the long-term evolution of this incising canyon?

6.1. Discharge measurements

Because Fossil Creek does not have an established discharge gage, we developed a discharge record for our two-year study period (July 2006 to July 2008). Stage was recorded using an Onset Hobo water level logger that we installed 3.3 km downstream of the diversion dam; the resulting data were corrected for atmospheric pressure fluctuations using an identical sensor installed in a nearby tree. We selected a straight, mixed bedrock-cobble-bedded reach, with minimal bank irregularities, and no travertine dams. A ~4 m bedrock step at the far downstream end of the reach prevents any backwater effect (a prominent tower of relict travertine guards the right bank of this step, inspiring us to name this the Sentinel reach). To build a stage-discharge rating curve we surveyed the channel and valley-bottom cross-section and slope with a total station, periodically measured velocity with FlowTracker ADV and Marsh-McBirney 201D current meters, used Manning's equation to extrapolate to higher discharges, and corrected for the travertine deposition we detected in the flow gage reach (Fuller, 2009).

Fig. 14A shows the time series of discharges calculated from the stage record at the Sentinel gage site over the 2 year study period beginning in July 2006. Also plotted for comparison is the discharge measured on the Verde River downstream of the junction with Fossil Creek (Verde River below Tangle Creek, USGS gage #09508500). The steady baseflow of ~1.2 m^3/s in Fossil Creek was interrupted by moderate floods caused by monsoonal convective storms in July and August of 2006 and 2007 and by several larger floods in the winter of 2007–2008 (Fig. 14A). The two gaps in our discharge record resulted from difficulties downloading data, but the Verde gage record and field observations suggest that baseflow prevailed during these periods.

To provide insight into the frequency of the erosional floods that occurred during our study period, we completed a Log–Pearson III analysis of peak flow data from the Verde River gage. The Verde gage recorded annual peak flows for 2007 and 2008 at the same times as those we documented on Fossil during our study period, including on

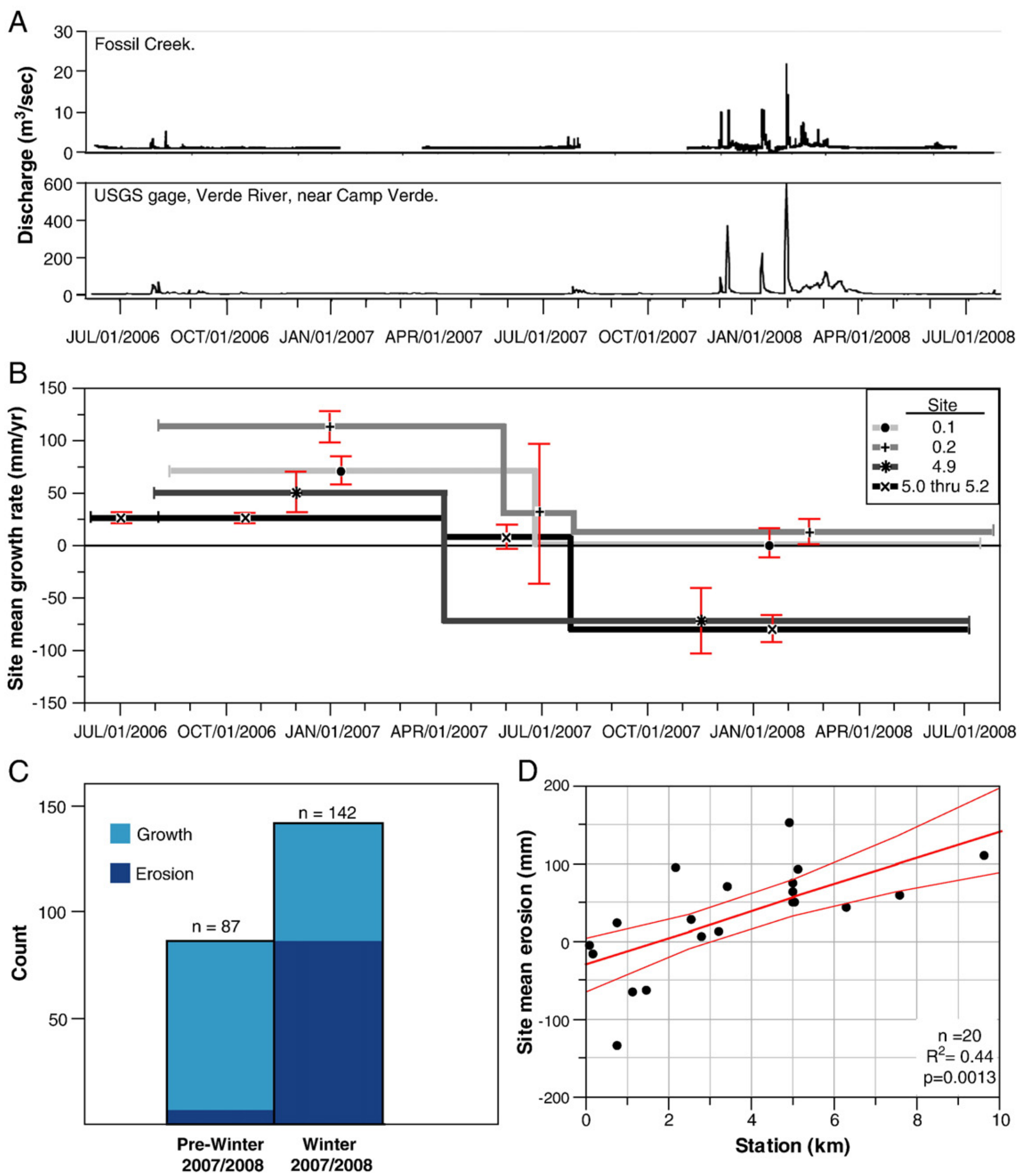

Fig. 14. Travertine erosion by floods. A) Time series of discharge measured over study period on Fossil Creek at Sentinel gage site and on Verde River at USGS gage near Tangle Creek. B.) Site-mean rates of vertical change for stations 0.1, 0.2, 4.9 and 5.0–5.2 km showing negative (erosion) or near-zero growth for measurement period encompassing floods of winter 2007–2008. C) Distribution of statistically significant growth and erosion measurements for time periods prior to and encompassing winter 2007–2008 floods. D) Variation in site-mean erosion depth for winter 2007–2008 period with distance downstream of diversion dam.

28 July 2007 of 38 m^3/s (the peak for that year) with a 1.1-year recurrence interval. As discussed above, this corresponded to the summer monsoonal event in Fossil Creek that caused minor erosion of travertine. The winter 2007–2008 peak, recorded on 28 January, reached 589 m^3/s and had a recurrence interval of 4 years; this corresponded to more a substantial erosion event in Fossil Creek. Although we cannot directly apply the flood frequencies from the Verde gage, which has a much larger contributing area, to Fossil Creek, the synchronicity of the 2007 and 2008 peak flows between the two sites suggest that the Verde flood frequency should have some correlation with Fossil Creek.

6.2. Temporal patterns of travertine erosion

During our two-year study period, erosive flood flows occurred in the summer monsoon season of 2007 and in the subsequent winter, when several rain-on-snow events caused widespread removal of travertine. Field observations during the high discharges of late summer 2007 showed that floods transform the waters of Fossil Creek from the shimmering, transparent turquoise hue of the carbonate-rich baseflow to a roiling, opaque brown of silt-rich runoff from the steep arid hillslopes. Boulder Canyon and Sally May Wash (Fig. 2), which are dry most of the year, were audibly transporting coarse bedload. Immediately downstream of the junction with Boulder Creek, in the aftermath of the floods, we observed the removal of a sequence of nascent travertine dams (site 9.4 km). The larger floods of the following winter caused more extensive erosion of travertine and changes in channel morphology. As detailed below, many dams containing magnets were damaged. At our downstream-most site (station 9.6 km), the channel avulsed, reoccupying an abandoned channel and burying the magnet-bearing travertine dams beneath clusters of boulders up to 0.5 m in diameter.

The measurement period encompassing the 2007–2008 winter floods had the greatest magnitudes of individual measured erosion rates and the largest numbers of magnets showing erosion. Where we measured net growth over this period, growth rates were generally lower than in previous periods for the same magnet. These results are illustrated in Fig. 14B, where we have plotted the site-mean growth and erosion rates for four sites, for each site-specific measurement period. In each case, positive growth occurred in the periods preceding the winter storms, despite the potentially erosive contribution of the summer monsoon storms of 2007. These data also illustrate the trend of decreasing growth rates and increasing erosion rates with increasing distance downstream. The area under the curves (in units of rate × time) is the measured magnitude of vertical change, which provides a more precise metric for comparing erosion between sites and time periods, because erosion occurs in brief events while growth is more sustained throughout the time period.

We detected some statistically significant erosion prior to the measurement period encompassing the winter 2007–2008 storms, presumably from the summer monsoon floods. Fig. 14C shows how erosion and growth were partitioned for the two time periods, for all magnets where we measured statistically significant vertical change. To obtain the largest number of significant measurements to compare in Fig. 14C, we average growth or erosion rates over the longest time period that either does or does not include the winter 2007–2008 floods; these periods vary somewhat from site to site (Figs. 10 and 14A). Of the 100 significant measurements in the pre-winter 2002–2008 period, only 9 showed erosion, while for the period including the winter floods, erosion occurred in 62% of the locations (88 out of a total of 142 magnets).

The temporal distribution of travertine growth and erosion over the study period is consistent with a bimodal magnitude–frequency relation as we hypothesized in Section 3. Growth dominates except when large, relatively infrequent storms occur. Moreover, the depth of erosion caused by the winter storms is significantly greater; for example, all of the magnets completely removed by erosion were lost during the winter storms. Although these results are encouraging, two years of monitoring is clearly not sufficient to quantitatively test the bimodal magnitude–frequency hypothesis.

6.3. Spatial patterns of travertine erosion

As suggested in Fig. 14B, a downstream trend occurs in the extent of travertine erosion observed following the winter storms. Fig. 14D shows the variation in site-mean erosion depth with station, for the measurement period encompassing the winter 2007–2008 floods. Of the 20 sites plotted here, 5 of the 6 upstream-most sites showed net growth, whereas all of the remaining downstream sites, spanning nearly 8 km of the study area, showed net erosion. Although the greatest site-mean erosion depth occurred at station 4.9 (a site with mature travertine just downstream of the Irving power plant and not far below the junction with a steep tributary channel), we observe an approximately linear trend of increasing erosion depth with distance downstream. We plot erosion depth (mm), rather than erosion rate (mm/year), because the shortest measurement period that includes the winter 2007–2008 storms varies between sites (Fig. 10). Note also that for the larger depths these are minimum estimates, because in the cases where magnets were entirely removed we calculated the erosion depth as the 10 cm length of the tube housing the magnet, plus any accumulated travertine growth from the pre-winter period.

Why do erosion depths increase with distance downstream? One possible explanation is the downstream increase in the drainage area supplying storm runoff and coarse sediment to the main-stem channel; flow downstream may simply have been deeper and more sediment laden, particularly at stations 9.4 km and 9.6 km which are below the junctions of two major tributaries (Fig. 2). The watershed area at the upstream end of the study area, however, is substantial (Fig. 2), and steep tributaries join Fossil Creek throughout its length, yet net growth was recorded during this period along the upper portion of the study area. A second explanatory factor could be differences in travertine strength, because of the rate and style of travertine deposition prior to the winter floods. Travertine deposited in the upstream portion of the study area may be denser than downstream, because of higher precipitation rates per unit volume of travertine accrual as a result of the greater degree of super-saturation. The downstream shift in biotic mechanism, from primarily autochthonous growth upstream to trapping of allochthonous litter downstream, could also contribute to progressive decease in travertine strength with distance from the spring source.

6.4. Interaction of travertine growth and erosion in long-term valley evolution

The morphodynamics of Fossil Creek present a paradox: at the millennial time scale the channel is actively cutting through bedrock, even though the dominant step-pool morphology reflects exuberant bio-mediated travertine growth. The travertine morphology may be particularly stable because of feedbacks active in the recovery of travertine dams from damage by erosive floods. For example, where notches or holes have been eroded into travertine dams, travertine deposition will be concentrated in the low point where flow is deepest and most turbulent, and narrow openings in damaged dams can be readily plugged by LWD; thus, the biotic and abiotic dynamics of travertine growth create a negative feedback to the perturbation of dam erosion. We can also speculate that the disturbance created by travertine erosion during floods could have a positive rejuvenating effect on ecosystem dynamics (Resh et al., 1988), with a corresponding increase in the intensity of biotic forcing of renewed travertine growth.

Considering the long-term evolution of the valley, it is reasonable to ask whether the biotic enhancement of travertine growth has any

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lasting effect; would the valley look different or incise at a different rate, if living organisms played no role in the channel dynamics? One possible answer is suggested by the relict travertine structures that are particularly prominent alongside the bedrock steps described above. The terrace adjacent to the left bank of the active channel (Fig. 6A) is the lowest of a vertical sequence of at least three terrace surfaces, each of which contains relict travertine structures that are increasingly weathered and degraded with height above the channel. For the terrace surfaces to be preserved, lateral shifts in the position of the active channel followed by vertical incision, must have occurred. We observe that the valley wall on the right bank, opposite the flight of terraces, is very steep, and lacks any remnant fluvial surfaces. Also, the relict travertine is commonly buried by sand on the upstream side, suggesting that when active the pools were effective sediment traps.

We hypothesize that runaway travertine dam growth has at times occurred in Fossil Creek, creating high dams (Fig. 3B) and long, deep pools, which reduce the erosional power of floods by trapping sediment that would otherwise provide abrasive tools (Sklar and Dietrich, 2004), and by dissipating flow energy in deep plunge pools. The point where large travertine structures abut the bedrock valley wall may represent a point of vulnerability, despite the greater strength of the bedrock, where lateral erosion in large floods could lead the flow to bypass travertine dam–pool system, cut vertically and leave behind abandoned, travertine-choked terraces. Runaway travertine growth is unlikely to occur in this environment without the acceleration of growth rates caused by the positive feedbacks created by biotic mechanisms for travertine accrual, given the erosive power demonstrated by the winter storms of 2007–2008. Hence, we conclude that the wide, and asymmetrical valley cross-section of Fossil Creek, may be a morphologic signature of life in this landscape (Dietrich and Perron, 2006). Without the role of living organisms in promoting travertine growth, the Fossil Creek canyon downstream of the springs would be narrower and perhaps also deeper, because of the more rapid and sustained bedrock incision that would be possible without the inhibiting effects of well-developed travertine dam–pool morphology.

7. Discussion

7.1. Linking Fossil Creek to conceptual models of ecogeomorphic feedbacks

Living organisms appear to play a central role in the 'life cycle' of the travertine dams of Fossil Creek, catalyzing dam formation, accelerating dam growth, and countering the erosive effects of large floods. The data supporting these interpretations, including trends in travertine organic content and rates of vertical change over time, show tremendous spatial variability, perhaps further evidence for strong biotic forcing. The substantial unexplained variability, however, could be reduced by improvements in our methods. For example, we primarily selected locations for magnet installation where travertine growth since dam formation already exceeded the 10 cm length of our magnet housing tubes. As a result, we may have missed the period of most rapid growth, and we also did not measure the growth of dams through lateral extension. Another source of variability is shifts over time in the local flow pattern through emerging travertine dam complexes. Locally rapid growth on an upstream dam can shift flow laterally, and change hydraulic conditions at magnet sites immediately downstream.

Each of the three frameworks for conceptualizing interactions between biological and physiochemical processes, introduced in Section 3, appear to be useful for interpreting travertine morphodynamics. An essential next step would be to quantify the relationships between biotic and abiotic factors and use numerical modeling to explore the system response. The three frameworks can be viewed as representing a hierarchy of complexity in modeling. In the first case, where biotic factors independently modulate the rates of mineral precipitation and travertine accrual, the challenge is to identify measurable biotic quantities that likely affect the biogeochemical environment resulting in small-scale differences in rates of travertine deposition. Yoo et al. (2005) have demonstrated this approach in modeling the influence of gopher population density and energy expenditure on hillslope sediment transport rates, arguably a simpler ecogeomorphic system. In the second case, to model the strength and influence of individual feedbacks, an additional set of functional relationships must be quantified, relating the dependence of ecosystem dynamics on geomorphic conditions. With relations established for the two-way coupling of biological and geomorphic processes, standard methods quantifying feedbacks can be applied to measure the strength of individual feedbacks and the stability of the system as a whole. The long-term stability of the travertine system, however, cannot be modeled without explicitly addressing the magnitude–frequency distribution of episodic disturbances. This will require quantifying additional functional relationships between flow magnitude, travertine age and morphology, and erosional efficiency, as well as ecosystem response to disruption of travertine-based dynamics.

Although travertine step-pool streams provide an ideal setting to explore the rich system behavior implicit in the three conceptual frameworks, these ideas should have potential application in a diverse set of environments with strong interactions between biology and geomorphology. For example, a bimodal magnitude–frequency relationship may be more appropriate than the classic unimodal dominant discharge framework, in modeling channels where growth of vegetation during baseflow stabilizes bars and banks that erode only during infrequent large discharges. Channel response to invasive species or changes in flow regime will depend on resulting shifts in the dynamics of the low-flow constructive phase as well as the high-flows when erosion occurs (Birken and Cooper, 2006; Sandercock et al., 2007).

7.2. Implications of ecogeomorphic feedbacks for stream restoration

Recognition of the potential for strong feedbacks between biologic and geomorphic processes is particularly important in rehabilitating rivers where habitat has been degraded by human intervention. The rapid regrowth of travertine triggered by the restoration of baseflow following dam decommissioning in Fossil Creek is an example of how feedbacks can be essential in determining the rate of ecosystem recovery. The restoration efforts at Fossil Creek exemplify emerging approaches to stream restoration focused on restoration of flow (e.g., Arthington et al., 2006) and sediment supply (e.g., Wright et al., 2008). This process-based approach may be especially effective in triggering or facilitating the types of ecogeomorphic feedbacks, and the associated rapid rates of ecosystem recovery, observed in Fossil Creek. This contrasts with the more common form-based approaches to stream restoration, in which a desired channel morphology, such as a sinuous meandering planform, is constructed and stabilized. Such 'stable' channel design may suppress positive and negative feedbacks, such as might occur between riparian vegetation, bank strength, and pool depth, that would drive the system toward a more ecologically valuable and dynamic state.

An alternative approach would be to embrace instability, and attempt to design restoration interventions that will launch the system to evolve most rapidly by catalyzing and engaging feedbacks. Designing river restoration projects to take advantage of ecogeomorphic feedbacks will likely require several resources (in addition to money), which are often in short supply: water, as focused on in emerging environmental flow efforts (Arthington et al., 2006); land, to provide riparian buffers and accommodate lateral migration; time, to allow feedbacks to develop, particularly over several flood cycles; and political willingness to live with uncertainty, because the scientific tools to make precise predictions of coupled ecogeomorphic system evolution are not yet well

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developed. Restoration projects, as in the example of Fossil Creek, are best approached as quasi-scientific experiments, where learning for application to the next restoration project is as important a goal as the specific habitat restoration objectives.

8. Conclusions

In this study we have taken advantage of the restoration of baseflow following dam decommissioning to explore the interactions of biotic and abiotic influences on regrowth of travertine step-pool morphology. We find that living organisms strongly influence the pattern of travertine dam formation, the rate of growth of existing travertine dams, and, thus, counter the effects of erosion by floods in controlling the evolving channel morphology. In particular, we document the substantial contribution of seasonal algal growth to travertine accrual along a bedrock step, where the putative abiotic feedback that leads to emergence of travertine dams is well-expressed. We find that the most rapid rate of growth of nascent travertine dams is associated with the *in situ* growth of emergent plants and algal mats, and trapping of coarse organic material. Where growth rates correlate with the hydraulic factors of flow depth and aeration, the pattern is opposite to that expected for a direct abiotic influence and more consistent with indirect biotic control. A downstream decrease in travertine growth rates correlates with a downstream reduction in travertine organic content, suggesting that spatial gradients in ecosystem processes may influence and respond to changes in channel morphology and water chemistry. These and other observations, coupled with the strong beneficial effect of travertine morphology on ecosystem dynamics, provide compelling evidence for a positive feedback between biotic and abiotic processes in driving travertine morphodynamics in Fossil Creek.

Erosion of travertine by floods opposes the tendency for positive feedbacks between biology and morphology to produce runaway growth of travertine dams. We document erosion during floods with recurrence intervals of 1 to 5 years and find that only the larger floods are capable of causing substantial erosion. We hypothesize that in Fossil Creek two distinct effective discharges occur: the constructive-phase baseflow during which most travertine growth occurs, and a characteristic rare destructive event capable of destroying travertine dams and reshaping the channel morphology. The strength of influence of life on travertine growth will directly affect the magnitude of the effective erosive discharge. Further work is needed to test whether this model is generally applicable in streams with strong biological influence on geomorphic processes.

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