DISSERTATION

BEAVER AS DRIVERS OF HYDROGEOMORPHIC AND ECOLOGICAL PROCESSES IN A MOUNTAIN VALLEY

Submitted by
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Graduate Degree Program in Ecology

In partial fulfillment of the requirements
For the Degree of Doctor of Philosophy
Colorado State University
Fort Collins, Colorado
Fall 2005

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY CHERIE JENNIFER WESTBROOK ENTITLED BEAVER AS DRIVERS OF HYDROGEOMORPHIC AND ECOLOGICAL PROCESSES IN A MOUNTAIN VALLEY BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

BEAVER AS DRIVERS OF HYDROGEOMORPHIC AND ECOLOGICAL PROCESSES IN A MOUNTAIN VALLEY

In aquatic and semi-aquatic environments of North America, beaver (*Castor canadensis*) affect landscape structure and dynamics at a level rivaled only by humans. The objective of this dissertation is to identify the influence of beaver dams on hydrologic, geomorphic, and ecological processes in a mountain valley. The influence of two in-channel beaver dams and a 10-year flood event on surface inundation, groundwater levels, and flow patterns was examined in a 1.5-km section of the Colorado River valley in Rocky Mountain National Park, Colorado during the summers of 2002-2005. The two beaver dams and associated ponds controlled surface water and groundwater flow patterns over a larger portion of the valley and for a longer duration than a 10-year recurrence-interval flood. Most importantly, the primary hydrologic effects occurred downstream of the dams rather than being confined to the near-pond area. The dams attenuated the expected water table decline in the drier summer months for 9 and 12 ha of the 56-ha study area. My results suggest that beaver can create hydrologic regimes suitable for the formation and persistence of wetlands on large floodplains. The mechanism of beaver meadow formation was also examined by measuring sediment deposition, nutrient availability and plant species cover in a 4.3-ha area of the valley that was hydrologically influenced by one of these beaver dams. The in-channel dam triggered overbank flooding in the study area, killing vegetation in areas that were deeply flooded and deposited ~750 m^3 of sediment on the floodplain and terrace west of the river. The study area formed a spatially heterogeneous beaver meadow after the dam failed and the area drained. Bare sediment was quickly colonized by *Carex utriculata* and *C. aquatilis* forming sedge-dominated communities on wet sites and early successional grasses such as *Critesion jubatum* and *Agrostis scabra* forming grasses-dominated communities on dry sites. Willow and aspen seedlings were found throughout the beaver meadow, suggesting that the sedge and grass plant communities may succeed to a shrub-carr community, facilitating future reoccupation of the site by beaver.

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I thank my parents for their unconditional love and encouragement. Their occasional financial contributions have taken the sting out of my academic habit. Many friends have helped me maintain a sense of balance during my time here in Fort Collins – I love you all. Thank you Travis for believing in me.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF APPENDICES

1. INTRODUCTION

1.1 Project rationale

In aquatic and semi-aquatic environments of North America, beaver (*Castor canadensis*) are the key ecosystem engineers (Gurney and Lawton, 1996) that affect landscape structure and dynamics at a level rivaled only by humans (Butler, 1995). They create aquatic habitat by building dams to restrict the flow of moving water (Naiman et al., 1986, 1988). Therefore, beaver possess the ability to alter landscapes both hydrogeomorphically and ecologically (Johnston and Naiman, 1987). Beaver-induced alterations to drainage networks are not unusual or localized, although populations were once greater than they are today. In North America their historic range was estimated to be 15 million km^2, including nearly all aquatic habitats from the arctic tundra to northern Mexico (Naiman et al., 1988).

The literature on beaver effects on hydrologic, geomorphic and ecological processes contains papers that analyze the effects of their dams and ponds on hydrologic processes such as stream velocity, hydraulic residence time, hyporheic flow underneath dams, local water tables, and creation and maintenance of riparian wetlands (review by Gurnell, 1998). Sedimentation studies have emphasized channel sediment accumulation rates and texture (Bigler et al., 2001), N and P sequesteration (Naiman and Melillo, 1984), and the formation and persistence of beaver meadows in low-energy environments (Remillard et al., 1987). However, research efforts thus far have often overlooked the influence of beaver in high-energy environments, which may encompass a much larger area than the pond itself. Visually, one can observe numerous beaver ponds in lower-gradient valleys within the Rocky Mountains. The abundance of beaver activities should have quantifiable impacts on the hydrology, geomorphology and plant communities in these valleys.

Rocky Mountain National Park is a good place to test ideas about beaver effects on hydrogeomorphic and ecological processes in higher-order rivers that are still small enough to be dammed. The Colorado River is the main drainage network on the west side of Rocky Mountain National Park. The river has a 1 % gradient and flows through a broad (~ 1 km wide) valley. Beaver in the valley can build dams across the river.

Previous research in the Colorado River valley and elsewhere in Rocky Mountain National Park has highlighted the key role of beavers in landform formation and riparian ecosystem functioning (Cottrell, 1995). For example, Cooper et al. (in press) showed that beaver dams have historically been critical for creating two of three landforms where willow recruitment occurs in Moraine and Horseshoe Parks. Gage (2003) found little willow recruitment at the same sites due, in part, to a lack of beaver. Without beaver, the geomorphic processes that create suitable landforms and hydrologic patterns for willow establishment are rare (Cooper et al., in press).

Visual observations and mapping surveys of beaver-created landscape features in the Colorado River valley in Rocky Mountain National Park indicate that beaver have historically influenced almost every portion of the valley (C. Westbrook, unpublished data). Relict beaver ponds, some that still hold water, are no longer connected to water sources large enough to have created and maintained them. The establishment processes that formed the extensive willow stands of the valley no longer occur. Soil cores removed during groundwater well installations since 1995 (S. Woods and C. Westbrook, unpublished data) are mottled well above the current water table, indicating that persistent soil saturation has occurred. These data suggest that the water table was previously much closer to the ground surface than at present.

1.2 Objectives

The main objective of this dissertation is to assess the impacts of beaver on hydrogeomorphic and ecological processes of mountain valleys in the Rocky Mountains of Colorado. This research examines the effects of beaver dams and low recurrence-interval floods on groundwater-surface water interactions, as well as fluvial landform formation and persistence. I intensively studied two beaver dams in the headwater of the main river in southwestern North America, the Colorado River within Rocky Mountain National Park, Colorado from May through late September/early October 2002 to 2005. The first paper (Chapter 2) compared the effects of beaver dams and low recurrence-interval floods on hydrologic processes in a mountain valley. I evaluated the influence of two different in-channel beaver dams and a 10-year recurrence-interval flood on surface inundation, groundwater levels, and flow patterns in a 1.5-km reach of the Colorado River near its headwaters. The second paper (Chapter 3) examines how beaver meadows form in a high-energy, montane riverine environment. The spatial distributions of overbank sedimentation, sediment nutrient content, nutrient availability, and initial composition of the vegetation was assessed following the failure dam of a beaver dam in an area that had been hydrologically affected by the dam. In Chapter 4, I discuss the importance of beaver in shaping riverine landscapes in North America to broaden the pond-centric focus of the literature to include beaver effects at the watershed scale. Specifically, I examined how beaver affect hydrologic, geomorphic, nutrient, and plant community dynamics of streams, floodplains, terraces, oxbows, and peatlands.

1.3 Beaver dams studied

Two beaver dams were intensively researched in this dissertation – an Upper Dam and a Lower Dam (Figure 1.1). The Lower Dam (Figure 1.2) was an L-shaped dam spanning the 10-m wide Colorado River. The dam was completed 24 August 1997 (Woods, 2001) and remained intact until it was breached by exceptionally high streamflow on 29 May 2003. The total dam length was 65 m, ranging in height from 0.7 to 1.7 m, and it consisted of willow and alder stems, mud, and river rocks. It diverted approximately 70 % of the river volume onto the floodplain within a week of its completion (Woods 2000). Beaver built a network of dams (~ six) and canals in the valley; these dams were 0.1 to 0.5 m high and 0.3 to 100 m wide.

A second beaver dam (Upper Dam, Figure 1.3) was built across the Colorado River in early October 2003 and breached on 04 June 2005. The Upper Dam was 0.8 m high and 8.0 m wide and consisted of alder and willow stems. The Upper Dam also diverted a large portion of its flow onto the floodplain and adjacent terrace following its completion, and beaver used this diverted water to build 12 dams in the valley that were similar in size to those built near the Lower Dam.

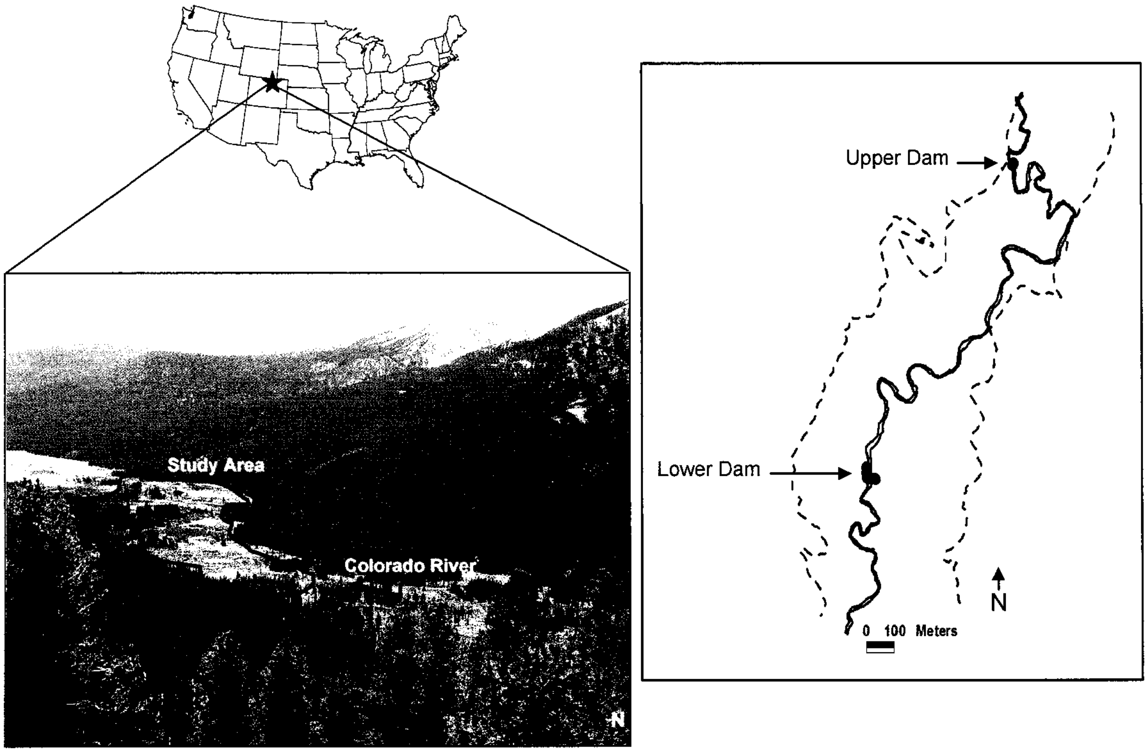

Figure 1.1 Location of the study area and the Upper and Lower Beaver Dam within the Colorado River valley in Rocky Mountain National Park, Colorado, USA (left). The dotted lines delimit the valley floor and the solid lines depict the Colorado River channel.

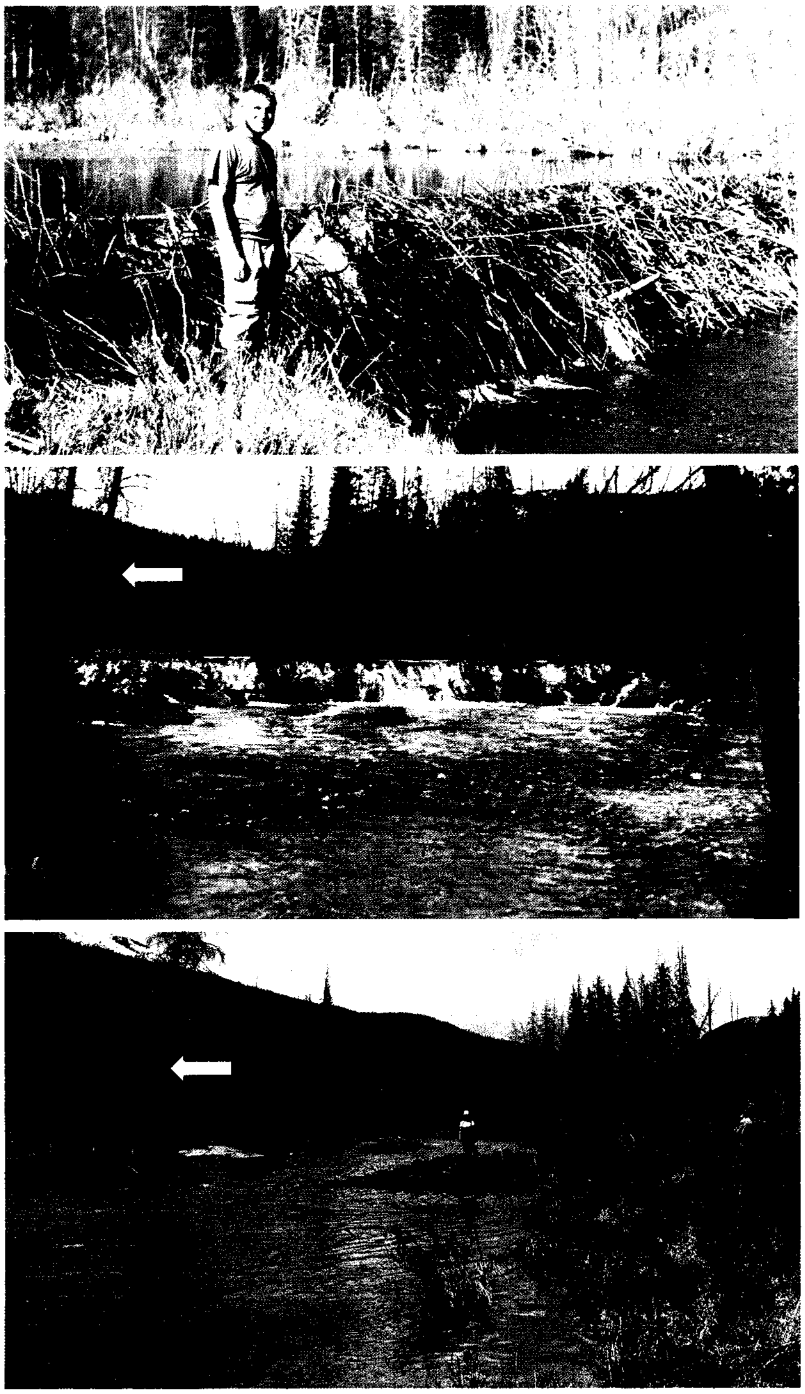

Figure 1.2 The Lower Beaver Dam in August 2002 (top), two days before its breach (middle) and one day after its breach (bottom). The arrows indicate the same tree in the middle and bottom photographs.

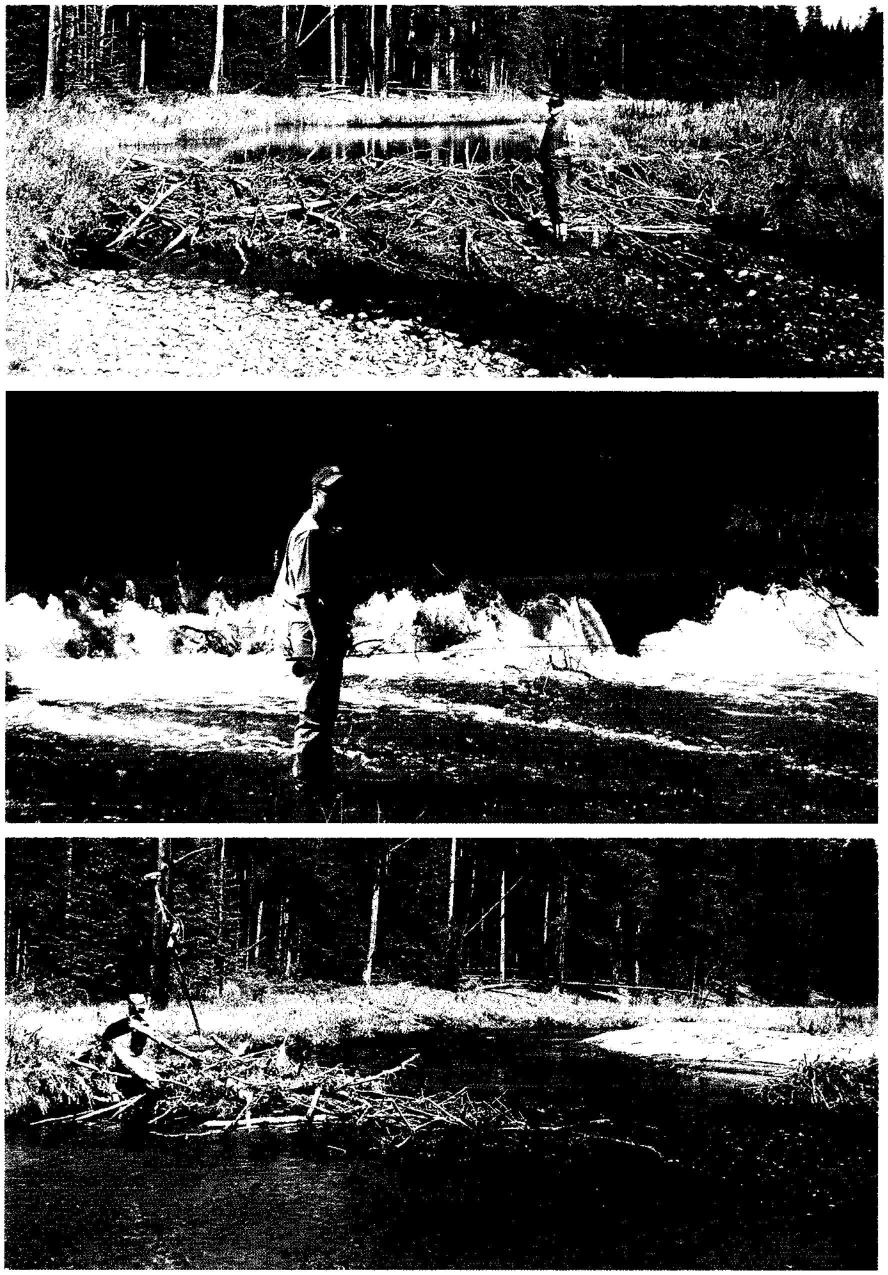

Figure 1.3 Photographs of the Upper Beaver Dam within a week of its completion (top), hours before its breach (middle), and a week following its breach (bottom).

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2. BEAVER DAMS AND FLOODS IN CONTROLLING HYDROLOGIC PROCESSES OF A MOUNTAIN VALLEY

2.0 Abstract

Overbank flooding is recognized by hydrologists as a key process that drives hydrogeomorphic and ecological dynamics in mountain valleys. Beaver are ecosystem engineers that some ecologists have assumed may also drive riparian processes, but empirical evidence is lacking. We examined the influence of two in-channel beaver dams and a 10-year flood event on surface inundation, groundwater levels, and flow patterns in a broad alluvial valley during the summers of 2002-2005. The study area is a 1.5-km reach of the fourth-order Colorado River in Rocky Mountain National Park (RMNP), Colorado, USA. The beaver dams and ponds controlled surface water and groundwater flow patterns over a larger portion of the valley and for a longer duration than did a 10-year recurrence-interval flood. Unlike previous studies, we found the main effects of beaver on hydrologic processes occurred downstream of the dam rather than being confined to the near-pond area. Beaver dams on the Colorado River caused river water to move around them as surface runoff and groundwater seepage during both high and low flow periods. The beaver dams attenuated the expected water table decline in the drier summer months for 9 and 12 ha of the 56-ha study area. This work provides empirical evidence that beaver can influence hydrologic processes more than overbank flooding during the period of peak flows, as well as low flows on the Colorado River, suggesting that beaver can create and maintain hydrologic regimes suitable for the formation and persistence of wetlands.

2.1 Introduction

Riparian areas are distinct from rivers and uplands because they have seasonally saturated soils that also can be dry for extended periods of time. The boundaries of riparian areas are often defined as extending outward from the stream bank to above the high water mark, and includes vegetation influenced by elevated water tables (Gregory et al., 1991). Complex interactions among river water, tributary streams, subsurface hillslope runoff, direct precipitation, and alluvial aquifers govern groundwater table dynamics in riparian areas (Winter, 1995; Patten, 1998; Burt et al., 2002a, b). Groundwater levels often decrease over the summer months due to the combined effects of evapotranspiration by riparian vegetation, reduced inputs from adjacent hillslopes, and lower river stage. In mountain valleys, groundwater levels may not recover until the following spring because snowmelt runoff provides the majority of annual streamflow and recharges hillslope aquifers. Understanding the mode of riparian area inundation and recharge of alluvial aquifers is critical for the management of river corridors.

Overbank flooding is a key hydrologic process controlling riparian water table dynamics and ecological processes such as biogeochemical cycling and plant diversity (Naiman and Décamps, 1997). Overbank flooding typically occurs for a few days to weeks once every 1 to 2 years for most natural rivers (Wolman and Leopold, 1957); this alternation of wet and dry phases enhances biotic diversity and productivity in the riparian area (Junk et al., 1989). River water also can be laterally transferred from the channel to the riparian area by infiltration into shallow alluvial aquifers, depending on the relative elevations of the river stage and groundwater tables (Winter, 1995; Mertes, 1997;

Chen and Chen, 2003). Soil water and groundwater recharge during overbank flooding is often greater than from river-aquifer interactions or precipitation events (Stanford and Ward, 1988; Workman and Serrano, 1999; Kingsford, 2000; Girard et al., 2003).

Beaver (*Castor canadensis* Kuhl) are ecosystem engineers (Jones et al., 1997) that may also control hydrologic processes in riparian areas of low-order rivers that can be dammed. Beaver dams raise river stage and can control the exchange of water and sediment between rivers and adjacent riparian areas (Woo and Waddington, 1990; Lowry and Beschta, 1994; Zav'yalov and Zueva, 1998). Where beaver dams span the entire valley the main hydrologic feature will be an upstream pond that elevates groundwater levels adjacent to the pond (Naiman et al., 1988). Where valleys are unconfined yet rivers are narrow enough to be dammed by beaver the hydrologic effects of beaver may extend far beyond the edge of the pond.

In this paper we compare the effects of beaver dams and floods as controls on hydrologic processes in a mountain valley. We examine the influence of two in-channel beaver dams and a 10-year recurrence-interval flood on surface inundation, groundwater levels, and flow patterns in the headwaters of the Colorado River in the central Rocky Mountains.

2.2 Methods

2.2.1 Study site description

We studied a 1.5-km section of the Colorado River valley in RMNP, Colorado, USA ($40^{o}22'$N and $105^{o}51'$W). The site is a broad, low-gradient (0.01 km km^{-1}), alluvial valley with a mean elevation of 2720 m (Figure 2.1). The upstream drainage area is 138 km^{2} and ranges in elevation from 2667 to 3944 m. The floodplain lies at an average elevation of ~1 m above the channel bottom and is 0 to 25 m wide. Most of the valley is a terrace 0.7 to 1.2 m above the floodplain (Woods, 2001).

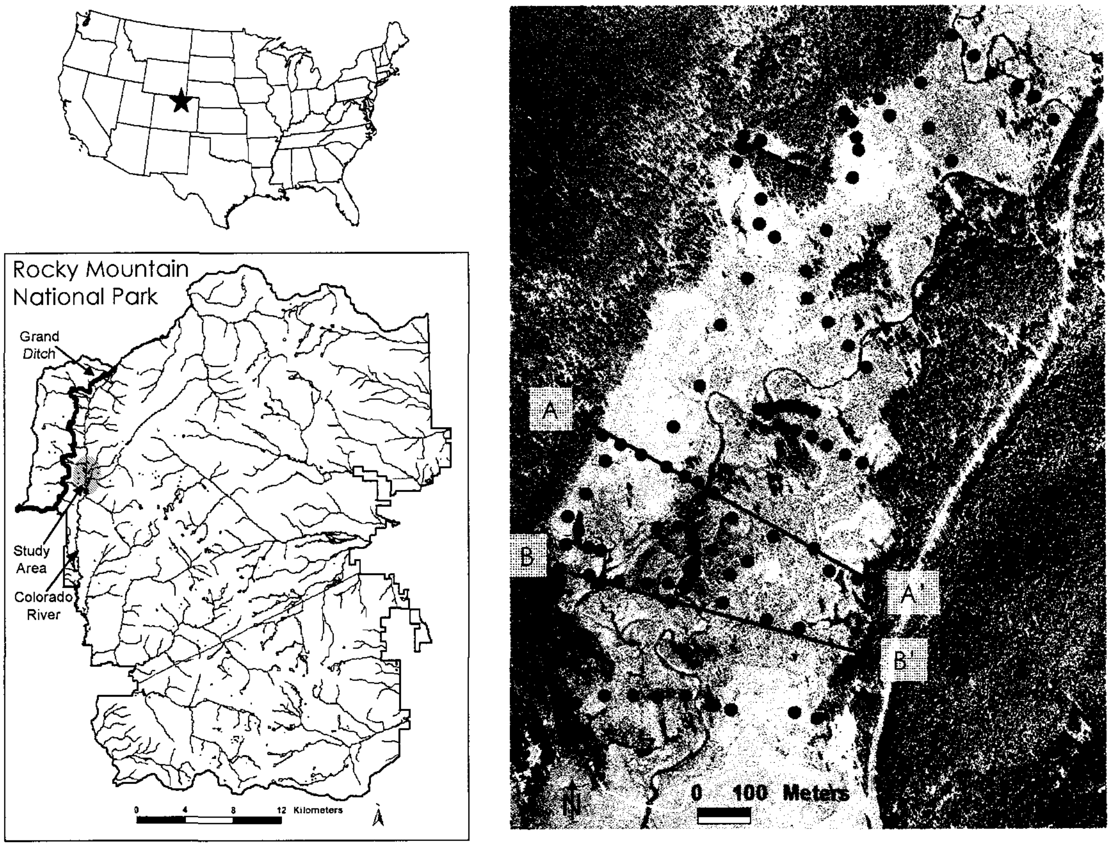


Figure 2.1 Location of the general study area in Colorado and in Rocky Mountain National Park, Colorado, USA (left) and a 1.5-km study reach of the upper Colorado River showing the location of 95 groundwater monitoring wells (black circles; right). Cross-sections A-A' and B-B' show the locations of groundwater wells used for Figure 5. The background aerial photograph was flown on 9 September 2001 and shows flooding at baseflow caused by the Lower Beaver Dam, which was built across the river about midway between the transect lines.

The valley is bordered by two mountain ranges that each rise ~1200 m above the valley floor. The Front Range on the east side of the valley consists of Precambrian metamorphic rocks and the Never Summer Range on the west side consists of upper Oligocene granitic magmas covered by an extensive lateral moraine deposited during the

Pleistocene glaciation (Braddock and Cole, 1990). Several alluvial fans are present along the hillslope margins. Mineral soils in the valley average 0.9 m thick, have silt loam and loamy sand textures, and hydraulic conductivities of 1 x 10^{-6} m s^{-1} to 3 x 10^{-8} m s^{-1}, determined using both falling and rising head tests (Fetter, 2001). Peat deposits of 0.3 to >1.5 m thick are present along the valley margins and have hydraulic conductivities of 2 x 10^{-6} to 4 x 10^{-6} m s^{-1}. Soils are underlain by 3 to 4 m of gravel alluvium that has a hydraulic conductivity of approximately 2 x 10^{-5} m s^{-1}. Below this gravel are 15-122 m of Holocene and upper Pleistocene alluvium (Braddock and Cole, 1990) of unknown hydraulic conductivity.

Mean annual precipitation in the watershed varies two-fold along the elevation gradient, from 560 mm at a location 16 km downstream of the study site to 1130 mm near mountain tops. Runoff in the valley is derived primarily from snowmelt, with periodic summer thunderstorms in July and August. Mean annual precipitation is 640 mm with 42 % falling as snow at the Phantom Valley SNOTEL station (CO05J04S, elevation 2750 m) and 885 mm with 84 % falling as snow at the Lake Irene SNOTEL station (CO05J10S, elevation 3260 m). Mean annual potential evapotranspiration (calculated using temperature data from 1949 to 2003 at the National Weather Service's Grand Lake 1NW weather station) in the valley is 430 mm, calculated using the Thornthwaite method (Dunne and Leopold, 1978). Evapotranspiration exceeds precipitation for May to September. The long-term mean December and July air temperatures at Grand Lake 1NW are -9.6 and 12.4 °C.

The Colorado is a fourth-order, meandering, pool-riffle river 5 to 15 m wide in the study area. Daily streamflow is markedly seasonal, varying from 1.8 m^3 s^{-1} during the late summer baseflow period to 14.7 $m^3 s^{-1}$ at maximum discharge during snowmelt. Beaver built an L-shaped dam (Lower Dam) across the Colorado River on 24 August 1997 (Woods, 2001), which remained intact until breached by high streamflow on 29 May 2003. The Lower Dam was 1.7 m high, 30 m wide, extended 35 m upstream along the west side of the river channel, and consisted of willow and alder stems, mud, and river rocks. It diverted 70 % of the Colorado River's flow onto the valley within a week of its completion (Woods, 2000). Beaver used this diverted water to build a network of dams (~ six) and canals in the valley; these dams were 0.1 to 0.5 m high and 0.3 to 100 m wide. A second beaver dam (Upper Dam) was built across the Colorado River during early October 2003 and breached on 04 June 2005. The Upper Dam was 0.8 m high and 8.0 m wide and consisted of alder and willow stems.

Vegetation in the valley is a mix of riparian shrublands dominated by *Salix monticola, S. geyeriana,* and *Betula fontinalis*, dry meadows dominated by *Deschampsia cespitosa* and *Calamagrostis canadensis*, and peat-accumulating fens dominated by *Salix planifolia* and *Carex aquatilis.* Hillslope vegetation is dominated by *Picea engelmannii* and *Abies lasiocarpa*. Plant nomenclature follows Weber and Wittmann (2001).

2.2.2 Precipitation and Colorado River discharge

Daily precipitation data were obtained from the Phantom Valley and Lake Irene SNOTEL stations; Colorado River discharge data were obtained from a U.S. Geological Survey (gauge #09010500) located 4.5 km downstream of the study site (elevation 2667 m). The watershed also is affected by the Grand Ditch, which has diverted 13 high-elevation tributaries out of the basin since ~1890 and reduced the average annual flow in the Colorado River by 29 % (Woods, 2001). A daily flood frequency curve was developed for 1954 to 2003 from the recorded discharge data, which accounted for diversion that reduced peak flow in 38 of 50 years in the historical record. A Log Pearson Type III distribution best represented the data. The U.S. Geological Survey estimated 2003 peak flow from a rating curve, as flows had overtopped the river banks; thus the 2003 peak flow and its recurrence interval are less accurate than for 2002 and 2004.

2.2.3 Flooding

The extent of flooding by the 2003 peak flow and by the 2002 and 2004 main-channel beaver dams in the valley were hand-sketched on low-altitude (1:4000) aerial photographs that were printed at a scale of 1:700. Ground-based photographs and the location of flood debris and fresh sediment were used to assist in delineation of overbank flooding following the event in 2003. The magnitude of floods required to produce overbank flooding similar to that achieved by the beaver dams were determined from a rating curve developed by *Woods* [2000] that correlated stream stage within the study reach to discharge at the U.S. Geological Survey stream gauge. The recurrence intervals of these floods were estimated from the flood frequency curve.

2.2.4 Groundwater flow patterns and water table fluctuations

We measured groundwater levels in 95 shallow monitoring wells situated in transects across the valley (Figure 2.1). Wells were constructed of 3.2-cm diameter, fully-slotted PVC pipe, capped at the bottom, and installed with a hand auger to the base of the soil column. Five wells were installed at ~1 m below the soil column where the water table frequently dropped into the underlying gravel alluvium during the summer. These wells consisted of a 3.2-cm diameter steel drive point (0.9 m screen) connected to threaded and slotted 3.2-cm diameter PVC or steel pipe. The UTM coordinates and elevations of wells were surveyed using a Trimble 5800 GPS that was accurate to 0.5 cm in the horizontal dimension and 1.0 cm in the vertical. Depth to the water table was measured weekly at each well between May and September 2002, 2003, and 2004 using a small dial voltmeter connected to two length-graded, exposed wires in close proximity that allowed an electric current to pass once they encountered water. Groundwater levels in well W24 were continuously monitored (25 May – 09 June 2005) before and after the Upper Beaver Dam failure using a WL14 pressure transducer (Global Water Instrumentation Inc., California, USA). Contour plots of water table elevations and maximum depth to the water table were derived by kriging point observations in Surfer version 7 (Golden Software Ltd., 1999). The average maximum depth to the water table was compared among years using a *t*-test with a Bonferroni correction for multiple comparisons in SYSTAT version 10 (SPSS Inc., 2000).

Hydrographs of hydraulic head versus time for individual wells were used to evaluate the response of the unconfined valley groundwater system to the Lower and Upper Beaver Dams. Agglomerative cluster analysis of well data used Euclidean distance and average linkage grouping methods to identify wells with similar patterns and magnitudes of water table elevations over time (Cooper et al., 1998). Only data for June and July were used in this analysis as they represented the period when the water table drawdown was greatest. Data were standardized to the ground surface and cluster analysis was used to group wells by the shape and magnitude of their hydrographs via PC-ORD version 4.14 (McCune and Mefford, 1999). Missing data were linearly interpolated if there were values before and after the missing value, otherwise the wells were excluded from the analysis. Wells were also excluded if the water table fell below the bottom of the well casing for extended periods of time; thus, the analysis used 72 of the 95 wells. Clusters were plotted as a layer in ArcView and the mean hydrograph for each cluster was computed. Data were examined to determine which wells changed clusters among years. Wells whose hydrographs were more stable and had a greater magnitude when the Lower Beaver Dam was intact (2002) than after it breached (2003) or when the Upper Beaver Dam was intact (2004) than before it was constructed (2002 and 2003) were considered to be influenced by a beaver dam. All other wells were considered not influenced by a beaver dam.

2.3 Results

2.3.1 Precipitation and stream discharge

Peak snow accumulation (as water equivalent) at the Phantom Valley SNOTEL station was 80 %, 115 %, and 58 % of average in 2002, 2003 and 2004. At the higher elevation Lake Irene SNOTEL station, peak snow water accumulation was 58 %, 103 %, and 60 % of average in these three years.

Mean daily discharge of the Colorado River 4.5 km downstream of the study site was 0.8 $m^3 s^{-1}$ (range 0.17 to 5.4 $m^3 s^{-1}$) in 2002, 3.7 $m^3 s^{-1}$ (range 0.3 to 22.7 $m^3 s^{-1}$) in 2003, and 1.8 $m^3 s^{-1}$ (range 0.4 to 11.6 $m^3 s^{-1}$) in 2004 (Figure 2.2). Peak flow recurrence intervals were 1.0, 9.6, and 1.6 yr for 2002, 2003, and 2004. Both 2002 and 2004 had very low spring peak flows while 2003 had a peak flow that was approximately four times greater than in 2002 and was the fourth highest peak flow on record. The large peak flow in 2003 was due to high early summer temperatures that triggered rapid melt of an above-average snowpack in the watershed above treeline. The 2004 peak flow was the result of an especially severe thunderstorm and was the only annual peak flow recorded that was not driven by snowmelt.

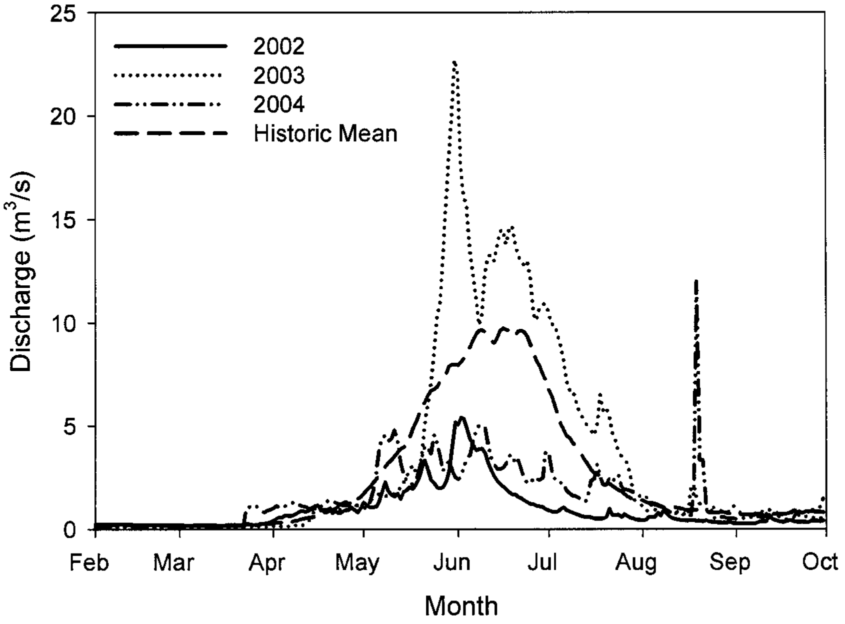


Figure 2.2 Colorado River mean daily discharge for 2002, 2003, 2004, and the historic mean (1954-2004). Recurrence-interval estimates for the 2002, 2003, and 2004 maximum daily peak flows are 1.0, 9.6, and 1.6 years. The 2004 peak flow was caused by very severe thunderstorms August 18-21.

2.3.2 Flooding

In 2002, Colorado River water flowed from the 0.1-ha Lower Beaver Pond obliquely across the western side of the valley, extending beyond the floodplain edge and onto the terrace (Figure 2.3a). Approximately 15 % of the study area (8.7 ha) adjacent to and downstream of the dam was inundated for the month following peak flow. A flood with a recurrence interval of >200 years would be needed to achieve a stream stage similar to that produced by the 1.7-m height of this beaver dam. The area flooded by the Lower Dam contracted as the Colorado River dropped to baseflow conditions in August when the river stage dropped below the western portion of the dam. Figure 2.1 shows areas that remained inundated through September 2002 as they were also inundated on 9 September 2001 when the valley was aerially photographed. Water that spread from the Lower Dam onto the terrace and floodplain returned to the Colorado River in eight separate locations, 70 to 500 m downstream of the dam.

In 2003, overbank flooding during peak streamflow inundated 10 % of the study area (5.8 ha), but the incursion of river water onto the valley was confined to a narrow zone adjacent to the river channel on the floodplain and oxbows (Figure 2.3b). Duration of the flooding in 2003 was much less than in 2002, and persisted for only 3 to 7 days. Flooding was also spatially variable as bank height varied greatly in the study reach.

The Upper Beaver Dam was present throughout the 2004 field season, creating a 0.2-ha pond, and like the Lower Dam diverted most of the Colorado River flow onto the valley floor (Figure 2.3c). Inundation of 21 % (12.0 ha) of the study area persisted throughout the summer because beaver did not increase the effective bank height by extending the dam upstream. A flood with a recurrence interval of at least 20 years would be needed to achieve a stream stage similar to the 0.8-m height of the Upper Beaver Dam. River water flowed from the pond southward down and across the valley and returned to the Colorado River in ten canals and channels located 350 to 930 m downstream of the dam. Beaver actively maintained some canals on the terrace, while some channels were in topographic lows formed by other processes.

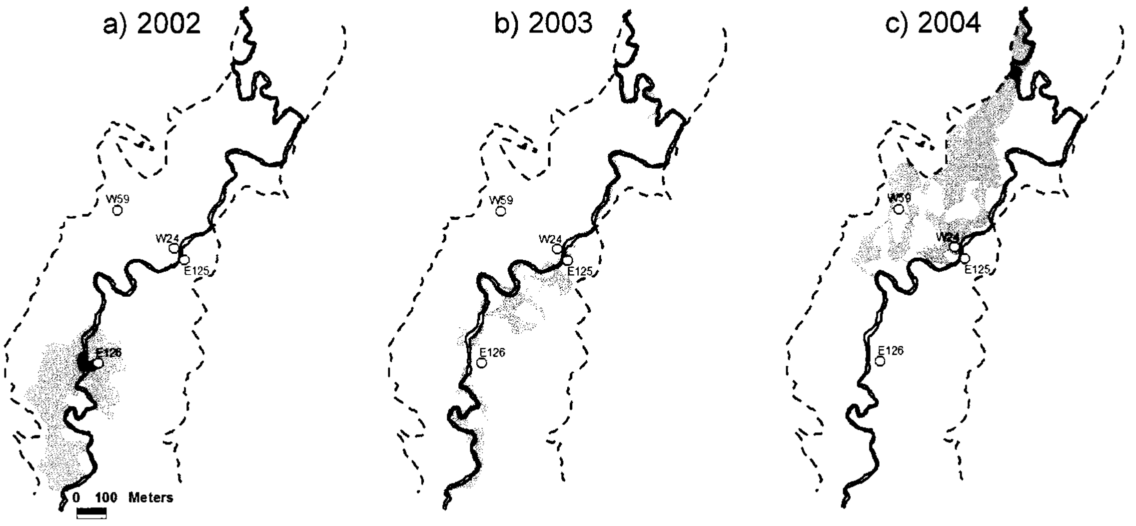
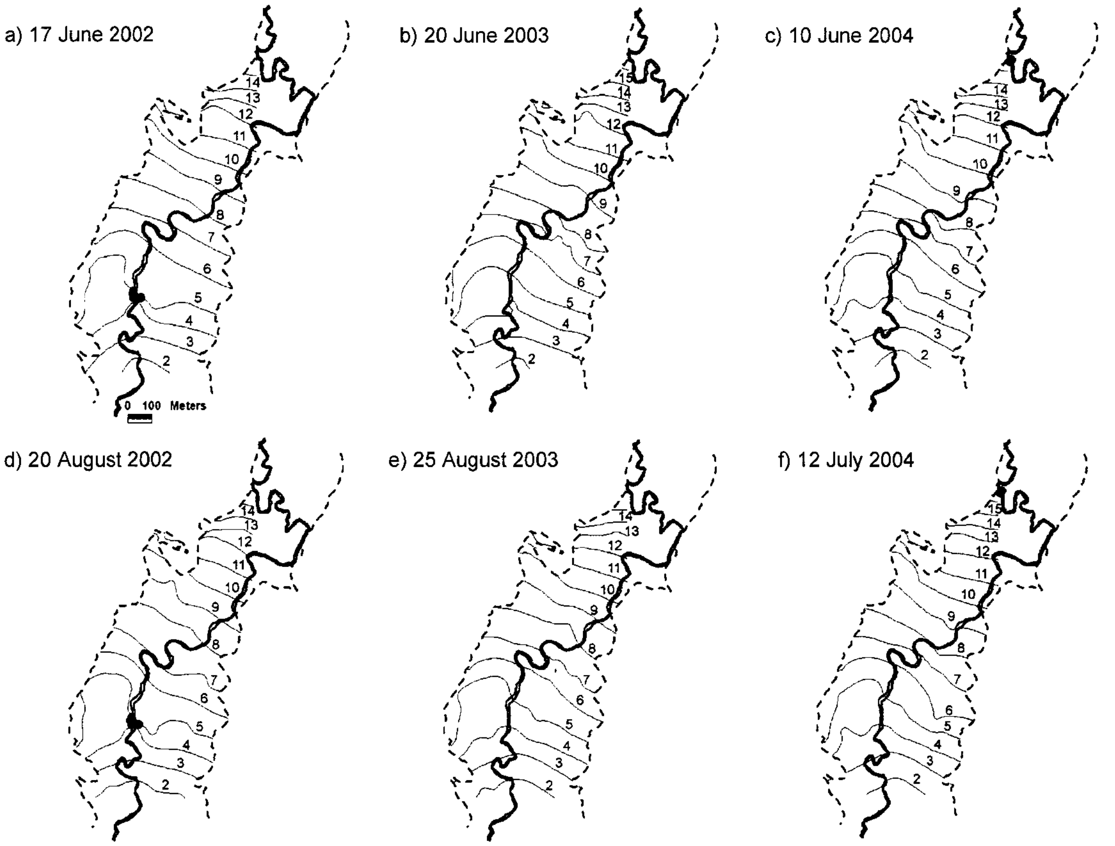


Figure 2.3 The 1.5 km study reach of the upper Colorado River valley showing maximum flooding (shaded) due to (a) the Lower Beaver Dam (thick black line) present in 2002; (b) the 2003 peak discharge; and (c) the Upper Beaver Dam (thick black line) present in 2004 (low peak discharge years and beaver dams present). Individual hydrographs of three wells (E126, E125, and W59) are presented in Figure 7 and a continuous hydrograph of well W24 for the week before and after the breach of the Upper Beaver Dam in 2005 is presented in Figure 8.

2.3.3 Groundwater flow patterns and water table fluctuations

The equipotential lines on the flownets were bent nearly parallel with the river channel in a localized area west of the Lower Dam (5.0 m isoline) during the high and low flow periods in 2002 (Figure 2.4a, d). Thus, groundwater flow was directed from the river channel southwest across the valley when the Lower Dam was present, which was similar to the direction of surface water flow in the same area. In contrast, in 2003 following the breach of the Lower Dam the horizontal flow direction was primarily down-valley during high and low flow (Figure 2.4b, e). The Upper Dam did not alter the direction of groundwater flow in 2004, but did cause a steepening of the down-valley groundwater flow gradient during both high and low flow (Figure 2.4c, f).


a) 17 June 2002

b) 20 June 2003

c) 10 June 2004

d) 20 August 2002

e) 25 August 2003

f) 12 July 2004

Figure 2.4 Groundwater flow patterns (isolines) for the Colorado River valley were derived by kriging well point data and show spring peak flow and low flow with (2002 and 2004) and without (2003) the presence of beaver dams (thick black lines). Isolines (1 m contours) are meters above an arbitrary datum and show that gradient for groundwater flow was mainly down-valley in absence of beaver or when the Upper Beaver Dam (2004) was parallel to down-valley flow. The Lower Beaver Dam (2002) was perpendicular to down-valley flow and the 5 m isoline west of the dam shows the flow gradient is away from the river.

In 2002, the groundwater surface was elevated during both high and low flow periods along the A-A’ transect, located ~100 m upstream of the Lower Dam (Figure 2.5a, b). A nearly flat groundwater surface extended laterally for about 80 m east and 12 m west of the pond where there were abrupt changes in the horizontal hydraulic gradient, particularly west of the pond. In 2003, groundwater flow was toward the river following the snowmelt period (June 20; Figure 2.5a) and away from the river in late summer (August 10; Figure 2.5b). In 2004, the groundwater flow gradient was away from the river during June and August (Figures 5a, b), and during the rest of the year (data not shown).

In 2002, groundwater levels near the stream channel remained stable and within 0.30 m of the ground surface along transect B-B', which was located ~120 m downstream of the Lower Dam (Figure 2.5c, d). Water levels remained near or above the soil surface in the middle portion of the valley both east and west of the river during mid and late summer. Water flowed from the middle of the valley in opposite directions toward the eastern hillslope and the Colorado River downstream of the Lower Beaver Dam, which indicated the presence of a groundwater mound in the middle of the valley. Water table elevation patterns were similar in 2003 and 2004, although water levels were consistently lower in 2004 when there was a shallower snowpack. The June water table was nearly level along transect B-B' during both 2003 (Figure 2.5c), when the Lower Beaver Dam was absent. By the second week of August in 2003 and 2004 (Figure 2.5d) a valley-wide decline in water levels had occurred.

Three distinct types of well hydrographs were identified using agglomerative cluster analysis (Figure 2.6). Cluster 1 had water levels that changed little during the summer and they were near the soil surface. Cluster 2 wells had water levels ~30 cm below the ground surface in spring and declined an additional ~35 cm during the summer. Cluster 3 wells had water levels ~80 cm below the soil surface in spring and declined an additional ~35 cm or more during the summer. Water levels in several cluster 3 wells were near the bottom of the well casing by late July in each year. Most wells were in clusters 2 and 3 during the dry years of 2002 and 2004; the only wells in cluster 1 were located in the area flooded by the Lower Beaver Dam (2002), Upper Beaver Dam (2004) or along the hillslope margins where ground water discharge occurred. All but five wells fell into clusters 1 and 2 in 2003. There were 9 wells within the area flooded by the Lower Beaver Dam that had higher and more stable groundwater levels in 2002 than in 2003 or 2004 even though 2003 was a much wetter year. Similarly, there were 12 wells within the area flooded by the Upper Beaver Dam that had higher and more stable groundwater levels in 2004 than in 2003 or 2002.

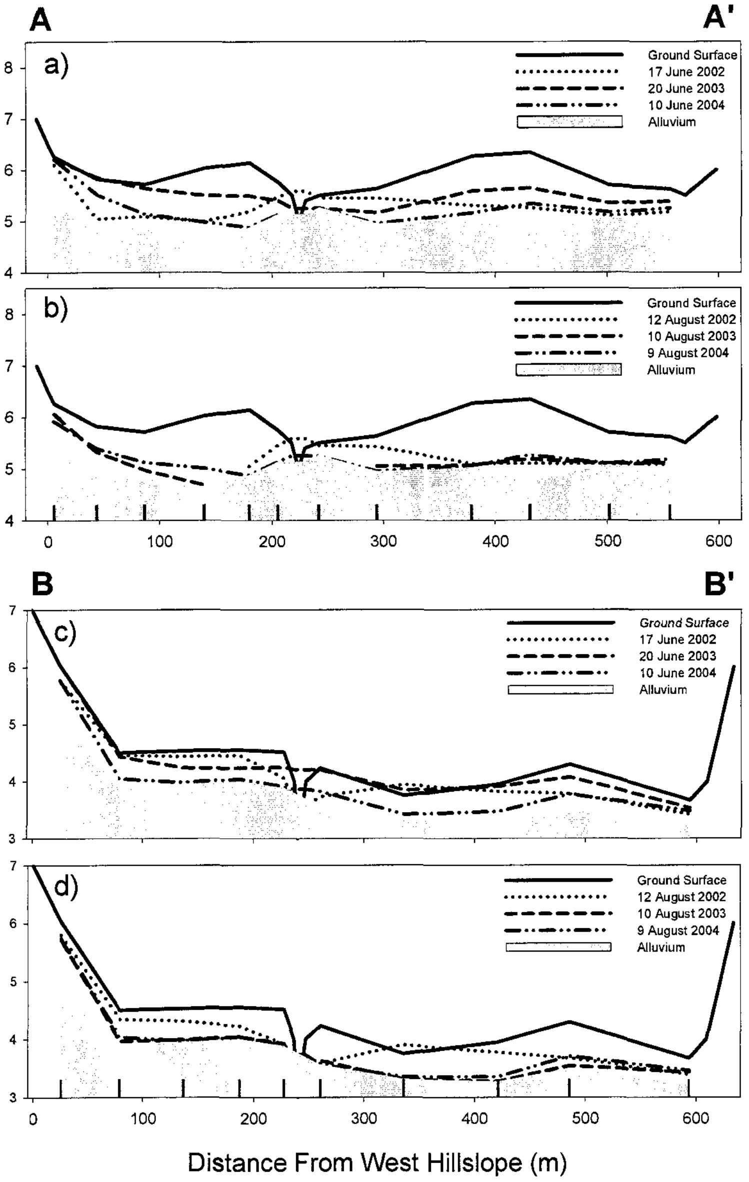


Figure 2.5 Groundwater levels following snowmelt (June) and during late summer (August) for upstream (a, b) cross-section A-A' (~100 m upstream of the Lower Dam) and downstream (c, d) cross-section B-B' (~120 m downstream of the Lower Dam). Vertical bars on b) and d) denote the location of groundwater wells used to estimate water levels along each valley transect. Horizontal groundwater flow was away from the river in the A-A' transect and groundwater levels remained near the ground surface in the middle of the valley in the B-B' transect when the Lower Beaver Dam was present in 2002, but not in 2003 or 2004.

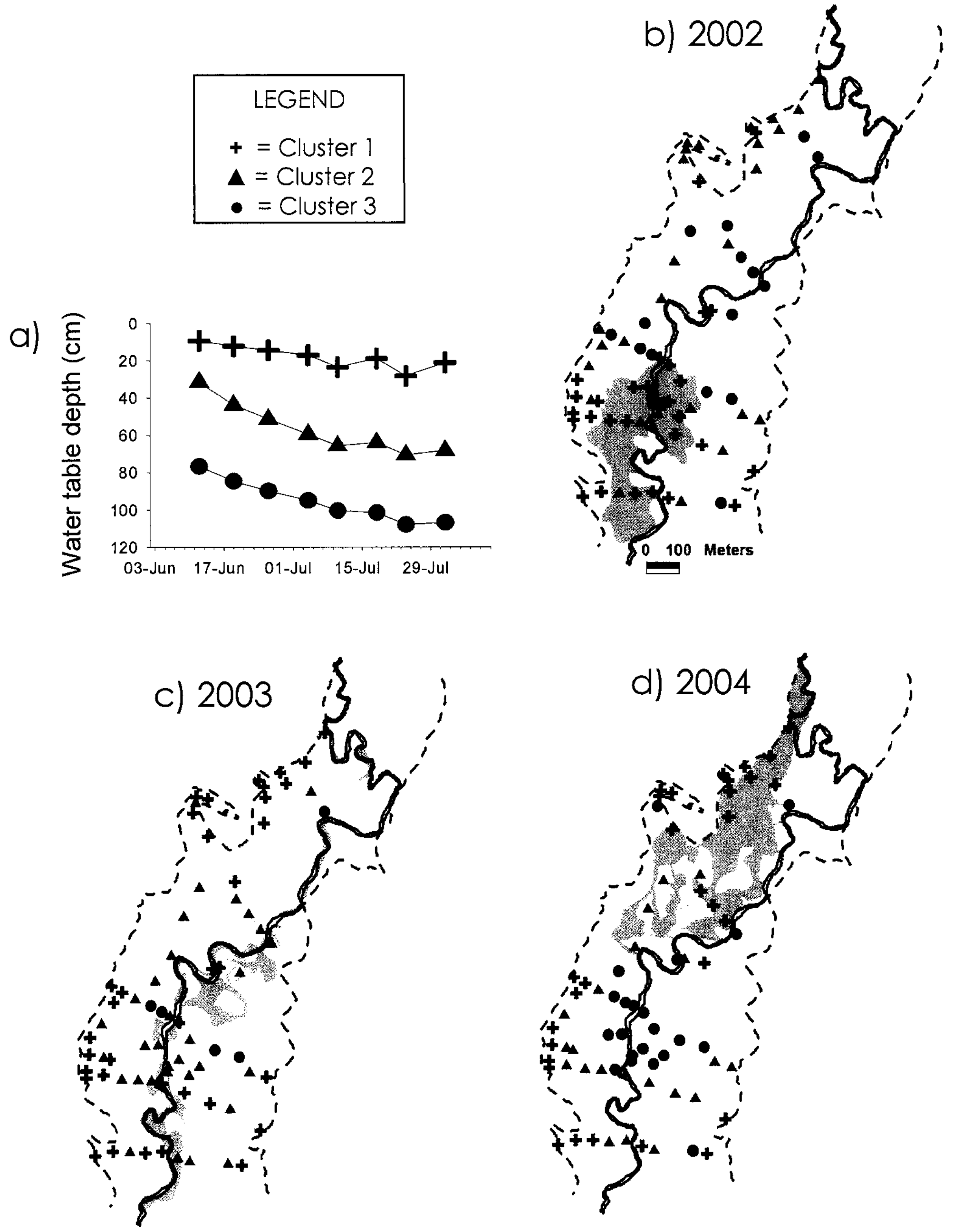


Figure 2.6 Maps (b-d) showing the results of the cluster analysis results (refer to methods for analysis details) during the water table drawdown period, illustrating how beaver dams controlled groundwater levels in 72 wells. Panel a) shows the mean hydrograph of all wells in each cluster. The grey shading shows extent of flooding attributed to the Lower Beaver Dam in 2002 (thick line), peak streamflow in 2003, and the Upper Beaver Dam in 2004 (thick line).

Fluctuations in water table elevations at wells E126, E125, and W59 were representative of seasonal variation in shallow groundwater of areas affected by the beaver dams or by overbank flooding during the study period (Figure 2.7). The highest groundwater levels in all wells occurred following peak flow in late May and early June. The water level in well E126, which was located 20 m east of the Lower Beaver Pond, remained stable and within 10 cm of the soil surface throughout the summer of 2002. However, the water level in this well declined by ~60 cm in 2003 when the Lower Dam was absent and water levels were approximately 40 cm lower throughout 2004 than in 2003. Well E125 was affected by neither beaver dam in 2002 and 2004, but overbank flooding occurred within 10 m of the well during 2003; the water table was below the bottom of the well throughout the 2002 and 2004 summers. Water levels in well E125 were within 10 cm of the surface during 2003 peakflow and declined to levels below the soil column by the end of July. The water table drawdown in well W59 was greater in 2002 than in 2003 likely because 2002 had a shallower snowpack and lower stream flow. In 2004 the ground surface near well W59 was flooded by the Upper Dam, which caused the water levels in well W59 to be higher than in 2002 and 2003 during low streamflow in July and August.

The failure of the Upper Beaver Dam on 04 June 2005 resulted in a rapid decline in groundwater levels throughout the area inundated. Continuous measurements of water levels were available for well W24, which was located 670 m downstream of the Upper Beaver Dam (Figure 2.8). Water levels in well W24 had a distinct diurnal fluctuation corresponding to the typical daily pulses in flow observed during snowmelt in the Colorado River (Figure 2.8) in the week preceding the Upper Dam failure. There was a rapid response of the water table 670 m downstream on the Upper Dam when it failed,

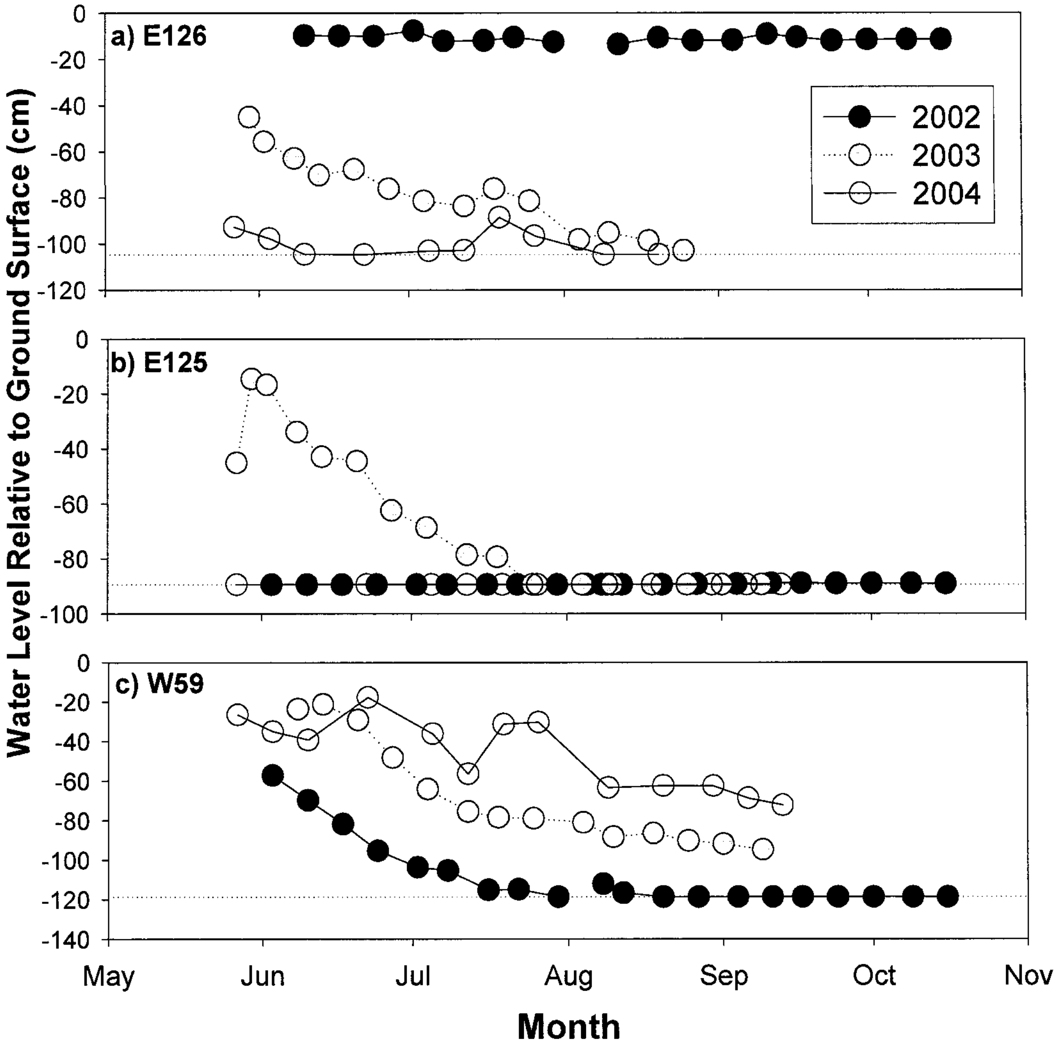


Figure 2.7 Hydrographs of three wells showing how either beaver dams (2002 and 2004) or overbank flow (2003) influenced water levels. The black circles in (a) are associated with the influence of the Lower Beaver Dam, the grey circles in (b) are associated with overbank flood that occurred in 2003, and the open circles in (c) are associated with the influence of the Upper Beaver Dam. The dotted line in each panel indicates the bottom of the well, so data points on this line may be at or below these values.

although there was no coincident change in Colorado River discharge. The water table declined approximately 8 cm in 14 hours. While there were no continuous groundwater level measurements made for the well beside the dam, weekly data showed a decline in water levels from 21 cm above the ground surface three days before the failure to 41 cm below the ground surface seven days after the failure.

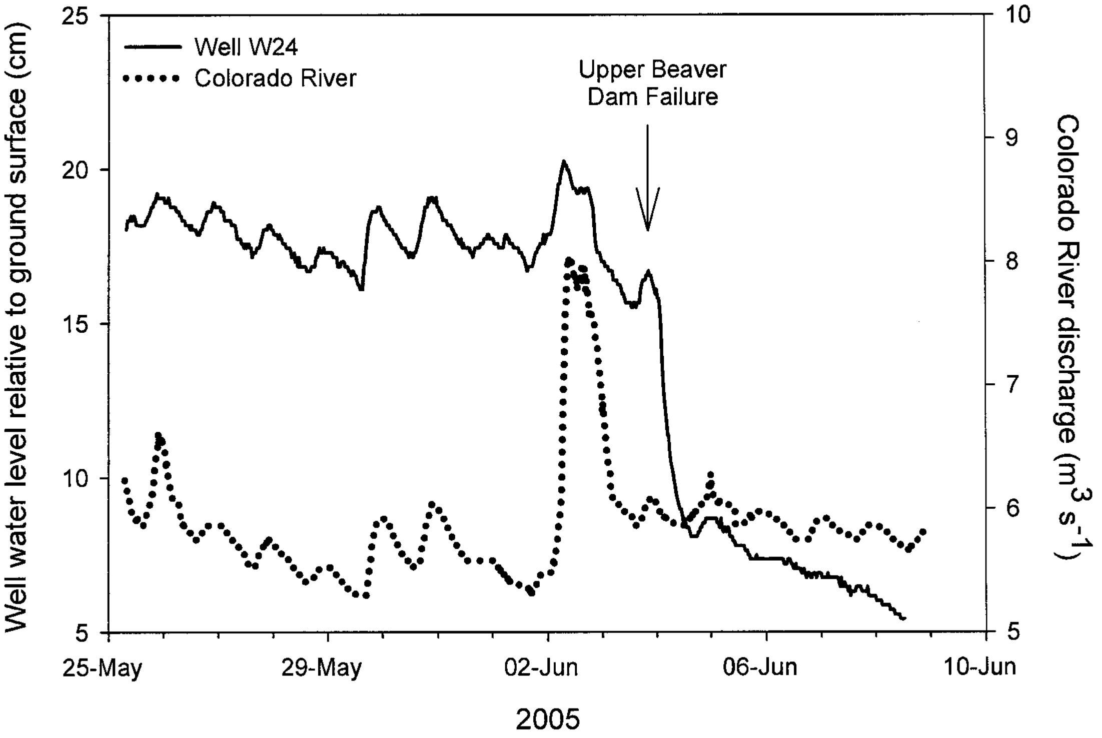


Figure 2.8 Groundwater levels in well W24 (located 670 m downstream of the Upper Beaver Dam) and Colorado River discharge before and after failure of the dam show the water table dropped about 8 cm during 14 hours after of the dam failed.

The date when the water table was deepest for the 95 wells in the study area occurred later in 2002 (27 August) than in 2003 (10 August) or 2004 (12 July), which indicates snowpack size and at some wells, the amount of precipitation received during late summer rain events are important controls on the amount of groundwater storage. Average maximum water table depth was similar in 2002 and 2003 (63 vs. 70 cm, *t*-test:

$P = 0.556$). The average maximum depth of the water table was 50 cm in 2004, which was significantly shallower than in 2002 ($P < 0.001$) and 2003 ($P = 0.037$). The mean drawdown, computed as the maximum minus the minimum water table, was 33 cm in 2002, 51 cm in 2003 and 26 cm in 2004, which reflected both the effects of beaver in the valley in attenuating the water table drawdown and differences in the amount of summer precipitation. There was considerable spatial variation in maximum water table depth among years. The maximum water table depth was within 40 cm of the ground surface in 46 % (27.0 ha) of the study area in 2002, 31 % (18.0 ha) in 2003, and 62 % (35.9 ha) in 2004. The areas with the highest maximum water table depths in 2002 were adjacent to and downstream of the Lower Dam. This was because Lower Dam raised the stage of the Colorado River 1.7 m, which caused river water to spill out of the channel, spread laterally, and flow down-valley. Areas with the shallowest maximum water table depths in 2003 occurred at the base of hillslopes where perennial groundwater springs supported peat soil development. The areas with the highest maximum water table depths in 2004 were downstream of the Upper Dam and along the base of the western hillslope.

2.4 Discussion

Beaver strongly affected hydrologic processes of the Colorado River, its floodplain and terrace near its headwaters in the Rocky Mountains. Beaver dams and ponds controlled surface water and groundwater flow patterns over a larger portion of the valley and for a longer duration than did a 10-year recurrence-interval flood. In-channel beaver dams created the hydraulic head necessary to raise water above the river banks and move it around dams as surface and groundwater flow during both high and low flow periods, spreading river water laterally and downstream of the dams. Each beaver dam attenuated the expected water table decline in the drier summer months over roughly one quarter of the 56-ha study area, whereas water tables fell non-uniformly throughout the study area when the dams were absent, even after a 10-year recurrence-interval flood. The results suggest that beaver dams can influence hydrologic processes of some mountain valleys more than overbank flooding.

2.4.1 Flooding

Overbank flood events have generally been regarded as the main hydrologic mechanism for replenishing groundwater and soil water in riparian areas (Workman and Serrano, 1999; Girard et al., 2003). The area inundated by the 2003 peak flow when beaver dams were absent was limited to a narrow zone immediately adjacent to the river channel. Flooding was confined mainly to the floodplain, inundating gravel bars and low-lying oxbows that were partially buried. The pattern of floodplain hydrologic connectivity we observed was consistent with the conceptual model of Tockner and Stanford (2002), which predicts that floods with a frequency of 1 in 10 years, such as the 2003 peak flow, should connect oxbows to rivers. Thus, streamflows with much lower recurrence-intervals are necessary to cause water to spill over the river banks and onto the riparian area.

Beaver create ponds that not only impound water but raise water tables adjacent to ponds via increased hydraulic head, area of soil-water interface, and duration of soil-water contact (Gurnell, 1998; Naiman et al., 1988; Hammerson, 1994). These processes can be limited in headwater valleys that are steep and narrow. In our study of an unconfined reach of the Colorado River, we found the main hydrologic effects of beaver were downstream of the dam rather than the upstream pond. The area affected by beaver extended hundreds of meters laterally and downstream of two in-channel dams that created the hydraulic head necessary to raise river water above the river banks, which substantially increased the probability of overbank flooding at a given stream discharge. Such extensive beaver effects are possible where rivers are small enough to be dammed and valleys are broad and flat enough to allow river water to spread across large areas. The flooded conditions in riparian areas affected by dams support the assumption that functional beaver dams can create and maintain extensive riparian wetlands.

The areal extent of flooding by the Lower and Upper Dams was controlled by a combination of height of the water ponded behind in-channel dams relative to height of river banks and a valley topographic relief that allowed beaver to create a network of off-channel dams, ponds, and canals on the surrounding terrace. These off-channel features allowed beaver to access new foraging areas and expand territories (Hodgdon and Lancia, 1983; Gurnell, 1998; Baker and Hill, 2003). This network resulted in the creation of multiple surface flowpaths (Woo and Waddington, 1990) that functioned like a braided river system to spread water across the valley. This water can alter plant composition and increase productivity in a fashion analogous to flood irrigation for hay production in the western United States (Peck et al., 2005). We found the dynamic flow of water and associated nutrient-rich sediment from the river channel to the terrace can form off-channel beaver meadows that greatly expanded the riparian zone (Westbrook et al., unpublished data).

Beaver flooded the valley throughout the streamflow recession and low flow periods, although the spatial extent of flooding produced by the Lower Beaver Dam decreased over the summer. Lowering of the pond water level below the top of the western portion of the dam caused water to mainly flow through the dam instead of overtop of it (c.f. Woo and Waddington, 1990). The area flooded by the Upper Beaver Dam was relatively constant throughout 2004 because the pond level was maintained at the top of the dam and water flowed around the dam onto the valley floor. Flooding could have been more extensive in wetter years such as 2003 than 2002 and 2004, if higher flows did not breach the dams.

It is unlikely that all water spilled from the beaver ponds returned to the river. Evapotranspiration rates were likely higher because beaver detained water by spreading it across the valley surface and ponding it behind numerous small dams on the terrace (Woo and Waddington, 1990; Burns and McDonnell, 1998). In addition, some beaver-distributed water likely recharged underlying alluvial aquifers in the valley, as the coarse-textured mineral soils had relatively high hydraulic conductivities (1×10^{-6} m s^{-1}) and the river water had a longer residence time in the riparian area because it was ponded behind off-channel dams.

2.4.2 Groundwater flow patterns and water table fluctuations

Higher groundwater levels and increased groundwater recharge were observed upstream of the Lower Beaver Dam in 2002, but not during the 2003 flood for the same area. Highly permeable channel sediments in association with relatively low hydraulic permeability of silt-loam riparian soils kept the hydraulic gradient oriented in the down-valley direction during the 2003 flood; a pattern that differs from the classic bank storage model, which predicts river water will be driven into the floodplain during bankfull events (Pinder and Sauer, 1971). High aquifer anisotropy has been shown to reduce lateral infiltration and maintain flow gradients parallel with the stream, thereby limiting water exchange between the river and riparian area (Chen and Chen, 2003). In contrast, the hydraulic gradient on the floodplain east and west of the Lower Beaver pond changed from a down-valley direction toward the valley center because of the increased elevation of stream stage behind the dam during the summer of 2002. Increased river-riparian soil interaction time due to the beaver dam appeared to compensate for the strong anisotropy of the system, permitting increased bank infiltration. Others have also found increased aquifer recharge upstream of a beaver dam (Lowry and Beschta, 1994; Triska et al., 2000) and a debris dam (Hill and Lymburner, 1998).

Groundwater levels indicated that water moved from the Lower Beaver Pond west (perpendicular to the river) into floodplain soils, then flowed south down-valley, and back east towards the river 300-600 m downstream of the dam. This pattern of groundwater flow was similar to the "looping" of groundwater flow around a beaver dam observed by Lowry and Beschta (1994) in central Oregon, but on a much larger scale. However, some researchers have found no influence of beaver activities on groundwater flow patterns. For example, Woo and Waddington (1990) found that beaver dams and ponds did not affect groundwater flow patterns in the subarctic wetlands surrounding James Bay, Canada because of the extremely low topographic relief. This suggests the groundwater flow effects of beaver activity may vary due to topographic relief or dam height, which can control the hydraulic gradient between the river and riparian area. The location of a beaver dam in relation to a valley's hydraulic gradient and confinement may also affect groundwater flow patterns. The Upper Dam in our study site had no effect on the direction of groundwater flow, as the dam was located parallel to the direction of groundwater flow and was situated in a relatively confined portion of the valley. Thus the efflux of river water was in the same direction as the valley groundwater flow gradient, which obscured the effects of the Upper Dam on flow direction. However, the presence of the Upper Dam steepened the down-valley hydraulic gradient for ~350 m south of the dam.

The recharge of underlying alluvium and evapotranspiration can deplete groundwater stored in the soil during the summer, as suggested by the valley-wide decline in groundwater levels we observed, that were frequently to the base of the soil column or into the underlying gravel alluvium. A low recurrence-interval flood was unable to maintain high water tables in the riparian areas throughout the summer, a time when riparian plant water demand and infiltration into the aquifer are high and streamflow is low. Beaver dams can reduce the effects of water table drawdown during the summer by constantly supplying water to the riparian area via surface and subsurface flowpaths. Elevation maps of minimum water table levels showed the Upper and Lower Beaver Dams sustained groundwater levels equivalent to or higher in 2002 and 2004 than in 2003, which had 30 % more snow water equivalent and a peak flow four times greater. This suggests beaver overcompensated for the lower spring runoff in 2002 and 2004.

Soil cores removed during the installation of our groundwater monitoring wells showed soil mottles above the elevation of the 2003 water table, which suggests soils had likely formed under conditions of long-duration soil saturation and anoxia. The mottles indicate that the water table was previously closer to the ground surface than during the conditions of 2003 when beaver-flooding was absent. The Colorado River discharge record shows overbank floods are too infrequent and too short in duration to explain the presence of mottled soils near the ground surface. The most likely explanation for soil mottle development is that beaver dams re-directed water across the valley floor and maintained waterlogged soil conditions for extended periods during past summers.

This study analyzed the effects of only two beaver dams (2002 and 2004) on hydrological processes in the study area. The beaver population in recent years (Mitchell et al., 1999), including during our study period, was only 5% of the 600 that were estimated to have been present in 1940 (Packard, 1947). Operation of the Grand Ditch has reduced summer flows in the Colorado River by ~50 % (Woods, 2000) since ~1890, which likely altered how beaver dams affected the hydrologic processes in the valley. Beaver were likely more abundant in the valley and elsewhere before they were trapped during the period of European settlement in the early to mid 1800s (Seton, 1929). If the results of our intensive study were extrapolated to a time of more abundant beaver then the magnitude of their hydrologic effects may have encompassed nearly the entire study area. It is easy to visualize abundant beaver as key drivers of hydrologic processes in mountain valleys and other unconfined stream valleys throughout North America. Their role as a hydrologic engineer likely applies to similar Eurasian ecosystems as well; although the dam-building behavior of Eurasian beaver (*Castor fiber* Linnaeus) is slightly less well-developed than for North American beaver (*Castor canadensis*) (Gurnell, 1998).

If beaver can drive hydrologic processes, and hydrologic processes drive soil and vegetation development, then beaver can develop and maintain wetland structure and function. Willows are the primary food and dam building material for beavers in our study area and in many other Rocky Mountain valleys. However, willows are declining sharply in RMNP due to excessive herbivory by elk (*Cervus elaphus*) and moose *(Alces alces*) (Peinetti et al., 2002; Baker et al., 2005, Gage and Cooper, 2005) and in other regions due to herbivory by these species and livestock (Baker and Hill, 2003). Without management to reduce competition for willows beaver could disappear and a critical driver of riparian area hydrologic regimes could be lost in RMNP and elsewhere.

2.5 Conclusions

This study provides several new insights about the hydrologic role of beaver dams versus floods in mountain valleys. A beaver dam on the Colorado River and associated terrace dams controlled the surface inundation, groundwater levels and groundwater flow patterns over a greater area and for a longer duration in 2002 than a 10-year recurrence-interval flood in 2003 when the dam was absent. In 2004, a second beaver dam built parallel with the down-valley groundwater flow steepened the groundwater flow gradient and created new surface water flow paths that inundated one-quarter of the study area. In both cases, water left the Colorado River, flowed across the floodplain and terrace, and then back to the river far downstream of the dams. Most importantly, we found that the main effects of beaver on hydrologic processes occurred downstream of the dams rather than being confined to the near-pond area. The presence of mottled soils near the ground surface throughout the study area suggests that hydrologic processes driven by beaver dams played a key role in maintaining waterlogged soil conditions for extended periods. The effects of beaver on hydrologic processes support the paradigm that they can create riparian wetlands.

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3. BEAVER MEADOW FORMATION IN A MOUNTAIN ENVIRONMENT

3.0 Abstract

Beaver are thought to play a key role in valley development through the layering of sediment-filled beaver meadows over millennia. While this process has been shown to occur in low-energy riverine environments, the mechanism for beaver meadow formation and thus valley development in high-energy riverine environments is currently unknown. We examined the mechanism of beaver meadow formation in a 4.3 ha area of the upper Colorado River valley, Rocky Mountain National Park, Colorado, USA during the summers of 2003 and 2004. An in-channel beaver dam triggered overbank flooding in the study area, killing vegetation in areas deeply flooded during the beaver occupation. Only plants on hummocks survived the flooding. Sediment accumulated on the floodplain and terrace west of the river (~750 m^3 of sediment) during the beaver occupation because the combination of the dam and a south-westerly valley slope created a strong hydraulic gradient in this direction. The deposited sediment remained following the breach of the dam and is protected from future re-mobilization by overbank flood events because the deposition areas are disconnected from the river channel unless beavers build another dam that reconnects them. Although nutrients were deposited in association with the sediment, the resultant landforms did not have higher nutrient availability than the surrounding landscape, likely because of the high sand content. Areas east of the river did not accumulate sediment, but the lack of vegetation meant that the mineral soil was exposed following the breach of the dam and de-watering of the study area. Bare deposited sediment and exposed bare soil was quickly colonized by sedge-dominated communities on wet sites and early successional grass-dominated communities on dry sites, forming a beaver meadow. *Salix spp.* and *Populus tremuloides* seedlings were

found throughout the study area, suggesting that the beaver meadow may succeed to a shrub-carr community, which would facilitate future reoccupation of the site by beaver.

3.1 Introduction

Beaver (*Castor canadensis* Kuhl) are key hydrogeomorphic and ecological agents that shape riverine landscapes by changing the availability of biotic and abiotic resources (Jones et al., 1997; Gurnell, 1998). Beaver accomplish this by building dams across low-order streams that pond water in order to provide protection from predators, expand foraging areas and territories, and store food over winter months (Hodgdon and Lancia, 1983; Gurnell, 1998; Baker and Hill, 2003). Beaver dam-building activities result in the transformation of terrestrial to wetland and lotic to lentic ecosystems, which alter patterns of sediment retention (Naiman et al., 1986), rates of soil nutrient cycling (Naiman et al., 1994; Johnston et al., 1995), organic matter and nutrient retention in the drainage network (Naiman and Melillo, 1984; Devito and Dillon, 1993), and vegetation succession (Terwilliger and Pastor, 1999).

Beaver dams function as efficient water and sediment traps, forming upstream ponds that fill with sediment over time (Naiman et al., 1988; Butler and Malanson, 2005). Dams can continue to retain sediment even when degraded or breached if they are located in a low-energy (c.f. Nanson and Croke, 1992) riverine environment (Butler and Malanson, 2005) or if there is a channel evulsion around the dam during beaver occupation (Cooper et al., in press). Ruedemann and Schoonmaker (1938) hypothesized that since the last glaciation, layering of sediment-filled beaver ponds throughout valleys has contributed substantially to valley formation by accumulating successive horizontal plains of sediment. Measurement of greater volumes of sediment in older vs. younger beaver ponds provides empirical support for their theory in low-energy riverine environments (Meentemeyer and Butler, 1999; Bigler et al., 2001).

The sediment retained in beaver ponds is thought to be generally fine-grained with high nutrient content (Ruedemann and Schoonmaker, 1938, Naiman et al., 1988). Nutrients are preferentially associated with fine-grained sediment particles (Walling and He, 1994; Steiger and Gurnell, 2002) and can be transported through transient sorption (Triska et al., 1994). Organic matter, such as wood debris from beaver-foraging expeditions and dead plants within the area flooded by the upstream pond, can further add to the accumulation of nutrients in beaver pond sediments (Naiman et al., 1986; Naiman et al., 1988). The anoxic conditions created by the wet hydrologic regime during beaver occupation leads to subsequent accumulation of nutrients in their reduced form (Pinay and Naiman, 1991). Thus, sediment-filled beaver ponds are thought to be nutrient-rich hydrogeomorphic features on the landscape.

Ponds drain after beaver abandon them and, in areas with flat topography, newly exposed sediments are quickly colonized by herbaceous plants such as sedges and grasses (Ives, 1942; Butler and Malanson, 2005). Drained ponds develop into gently sloping meadows that many researchers have termed beaver meadows (Johnston and Naiman, 1987; Meentemeyer and Butler, 1999). These meadows are relatively distinct, homogeneous patches that add to landscape heterogeneity by providing an opportunity for different plant species to establish on the nutrient-rich sediment (Remillard et al., 1987; Wright et al., 2002). Few beaver meadows succeed to riparian conifer forest and instead persist for decades to centuries on the landscape as herbaceous patches that may eventually be re-colonized by beaver (Neff, 1957; Barnes and Dibble, 1988; Naiman et al., 1988; Terwilliger and Pastor, 1999). It is this layering of beaver-created patches that Ruedemann and Schoonmaker (1938) believed significantly contributed to valley development.

However, beaver dams located in high-energy riverine environments tend to fail, which results in flushing of stored sediment downstream rather than development of beaver meadows (Meentemeyer and Butler, 1999). The theory of beaver-assisted valley development thus remains largely unknown in these landscapes, particularly in mountain regions. For Ruedemann and Schoonmaker's hypothesis to apply across varied landscapes, beaver must be able to create meadows by alternate processes in higher-energy riverine environments. Beaver meadows could potentially be located in parts of the landscape other than upstream of dams. Recent work has shown that in-channel beaver dams create the hydraulic head necessary to raise water above the river banks and move it around dams, spreading it laterally and primarily downstream where valleys are unconfined yet rivers are narrow enough to be dammed (Lowry and Beschta, 1994; Westbrook et al., submitted). Beaver-caused diversion of water onto floodplains and terraces may therefore lead to accretion of sediment on them. Such new landforms have the potential to transform into beaver meadows that may be nutrient-rich. Further, they may have a more spatially heterogeneous plant community than meadows that develop from sediment-filled beaver ponds because of the variable pattern of sediment accumulation on the landscape.

This paper examines whether beaver meadows form in montane riverine environments. If so, I ask: 1) where is sediment deposited in the landscape that drives beaver meadow generation; 2) are these meadows nutrient-rich compared with the surrounding landscape; and 3) are these meadows homogeneous vegetation patches?

3.2 Study area

The study was conducted within a riparian area adjacent to the Colorado River in Rocky Mountain National Park, Colorado, USA (40°22'N and 105°51'W) (Figure 3.1). The site is a broad, low-gradient (1 %) alluvial valley that has a mean elevation of ~2720 m and is bordered by two mountain ranges rising ~1200 m above the valley floor. The Front Range on the east side of the valley consists of Precambrian metamorphic rocks and the Never Summer Range on the west side consists of upper Oligocene granitic magmas covered by an extensive lateral moraine deposited during the Pleistocene glaciation (Braddock and Cole, 1990). Several alluvial fans are present along the hillslope margins. Historic evidence of beaver dams is present throughout the valley.

The Colorado River is a fourth-order regulated river with a snowmelt-driven hydrologic regime. Mean daily discharge ranges from 14.7 $m^3 s^{-1}$ in the spring to 1.8 $m^3 s^{-1}$ during baseflow. Suspended sediment concentrations in the Colorado River measured by the U S Geological Survey at gauging station #09010500, which is 4.5 km downstream of the study site range, between 0.5 and 217 mg L^{-1}. These measurements are infrequent, but sampling covers the range of discharge. The floodplain lies at an average elevation of ~1 m above the channel bottom and is 0 to 25 m wide. The rest of the valley is a terrace that lies 0.7 to 1.2 m above the floodplain (Woods, 2001). Mineral soils in the valley average 0.9 m thick and range from silt loams to loamy sands.

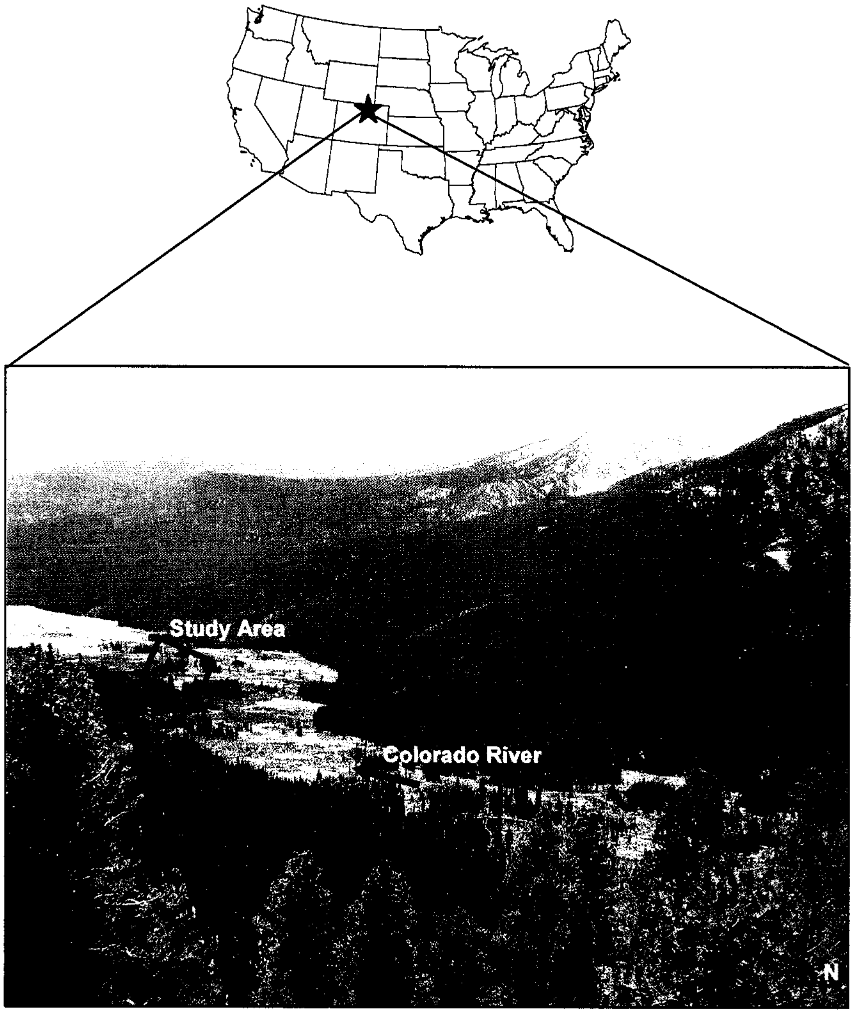


Figure 3.1 Location of the study area in the Colorado River valley within Rocky Mountain National Park, Colorado, USA.

Beaver built an L-shaped dam across the Colorado River on 24 August 1997 (Woods, 2001), which remained intact until breached by high streamflow on 29 May 2003. The dam was 1.7 m high and 30 m wide and extended 35 m upstream along the west side of the river channel. It consisted of willow and alder stems, mud, and river rocks. It diverted 70 % of the Colorado River volume onto the floodplain and terrace within a week of its completion in August 1997 (Woods, 2000) and flooded 8.7 ha in 2002 (Westbrook et al., submitted). Water that spilled from the beaver pond returned to the Colorado River in eight separate channels that were located 70 to 500 m downstream of the dam (Westbrook et al., submitted).

Vegetation in the study area prior to the creation of the beaver dam was a mix of riparian shrubland dominated by *Salix monticola, S. geyeriana, S. drummondiana, S. wolfii,* and *S. planifolia*, and dry and wet meadows dominated by *Deschampsia cespitosa, Calamagrostis canadensis*, and *Carex utriculata.* Plant nomenclature follows Weber and Wittmann (2001).

3.3 Methods

A non-aligned, systematic sampling design was used to analyze how beaver meadows form in a mountain environment. UTM coordinates of the corners of a 180 m x 240 m area known to be hydrologically affected by the beaver dam were obtained from a geo-referenced 2001 aerial photograph in June 2003. The study area was gridded into 10 x 10 m cells and the UTM coordinates of the center of a 1 x 1 m plot within each cell (n = 432) was randomly generated using a macro in Excel (Microsoft Corporation, 2002). A GPS with a horizontal accuracy of 2-4 m was used to find the center of each plot and this point was marked by a nail wrapped in flagging tape (Figure 3.2a). Thirty-one plots were not used as they were within the active river channel or a deep-water oxbow. A 1 x 1 m sampling quadrant was centered on the nail at each of the remaining 401 plots.

A reconnaissance survey was used to measure sediment accumulation at each plot (Brown, 1987). The sampling quadrant was subdivided into four 0.5 x 0.5 m sub-quadrants. Sediment thickness was sampled with a hand-held corer at the visually highest and lowest elevation in each sub-quadrant in August 2003. The core was visually inspected to locate the interface between the recently deposited sediment and the buried soil. Sediment lacked roots and soil had either roots or mottles present. Mean sediment thickness was determined by averaging the four high and four low spots in each plot. A two sample *t*-test of all 401 plots showed sediment thickness was not different between the high and low spots ($P = 0.87$), so the eight thickness replicates were averaged to yield one value for each plot. Sediment thickness was re-sampled at 20 randomly chosen plots to test our precision in identifying the sediment-soil interface. A paired *t*-test showed sediment thickness did not differ between the original sampling and re-sampling of the 20 plots ($P = 0.29$).

The eight sediment cores for each plot were aggregated in a polypropylene bag and taken to the laboratory for physical and chemical analysis. The cores were dried at 60 °C for 5 days and particle size for one sample from each plot was determined via the hydrometer method (Gee and Bauder, 1986). Five to ten grams of dried sample from each plot were hand-ground and analyzed for total organic carbon (TOC) and total nitrogen (TN) on a LECO CHN1000 analyzer (LECO, St. Joseph, Michigan, USA). Total phosphorus was measured by conducting nitric-perchloric digests on samples and then analyzing the digests by inductively coupled plasma at the Soil, Plant and Water Testing Lab at Colorado State University.

The ion exchange resin bag technique (Binkley, 1984) was used to assess the bio-availability of nitrogen and phosphorus 13 months following the breach of the beaver dam in May 2003. Resin bags were prepared by sealing 14 mL of anion resins and 14 mL of cation resins in separate pouches of a nylon stocking. A bag was buried at a depth of 5 cm in the center of each plot between 08 June and 23 August in 2004. Resin bags were recovered from 181 (45 %) of the 401 plots; bags were not recovered from 220 plots where the flagging was missing due to elk, moose, or other causes. Recovered bags were desorbed in 100 mL 2 M KCl and shaken mechanically for 1 h. The KCl extracts were filtered through Whatman #42 filters and frozen for later analysis. Thawed extracts were analyzed for total inorganic N (NH_4^+-N plus NO_3^--N) and PO_4^{3-}-N colourimetrically on an Alpkem automated flow system.

The plant species in each 1 x 1 m quadrat were identified for 393 plots in August 2004. Percent canopy cover was estimated for each plant species using six classes (<1, 1-5, 6-25, 26-50, 51-75, and 76-100 percent). The number of *Salix* spp. and *Populus tremuloides* seedlings present in each plot was also recorded. Hydrologic condition during the last three years of beaver occupation and post beaver occupation was evaluated for each plot using a combination of water table elevation maps (Chapter 2), aerial photographs, and still photographs. The four hydrologic condition classes were permanent standing water, seasonal standing water, water table seasonally near soil surface, and deeper water table.

Kriging was used to spatially interpolate the surface elevation in the study area. Kriging also was used to model the spatial variation in sediment thickness and texture (percentage of silt plus clay) and calculate the total amount of sediment deposited on the floodplain and terrace. Correlations among sediment thickness, texture, resin-nutrient content, N and P bio-availability, and number of *Salix* seedlings were explored using Pearson correlation coefficients. Significant correlations were further examined using regression analysis.

Multivariate statistical analyses were used to examine relationships among the vegetation samples based on canopy cover of species in each plot. A primary matrix containing species percent cover (midpoint of cover classes) within the 393 plots and for the 82 plant species was constructed. Six plots had < 1% plant cover and were removed from the data set prior to analysis. Major gradients in vegetation composition were identified using Detrended Correspondence Analysis (DCA). Agglomerative cluster analysis with Sorensen distance was used to create the dissimilarity matrix and average linkage grouping method to construct the dendrogram. Two plots were removed from the analysis because they had 100 % cover of one species (either *Picea engelmanii* or *Salix spp.*) and formed their own clusters. Indicator analysis was used to identify significant ($P < 0.05$) indicator plants in each cluster. We then correlated the 1st and 2nd DCA axes with environmental variables (sediment thickness, hydrologic condition during the last three years of beaver occupation, hydrologic condition post beaver occupation, resin-$N_{inorganic}$, and resin-P) using Pearson correlation coefficients. Significance was accepted at $P < 0.10$ because one hydrologic variable could not capture the complexity of the pre, during, and post beaver occupation hydrologic regime. Rather, one or several hydrologic regimes were important in evaluating plant community structure. Surfer version 7 (Golden Software Ltd., 1999) was used for kriging, PC-ORD version 4.14 (McCune and Mefford, 1999) was used for vegetation species composition analyses, and SYSTAT version 10 (SPSS Inc.) was used for other statistical analyses.

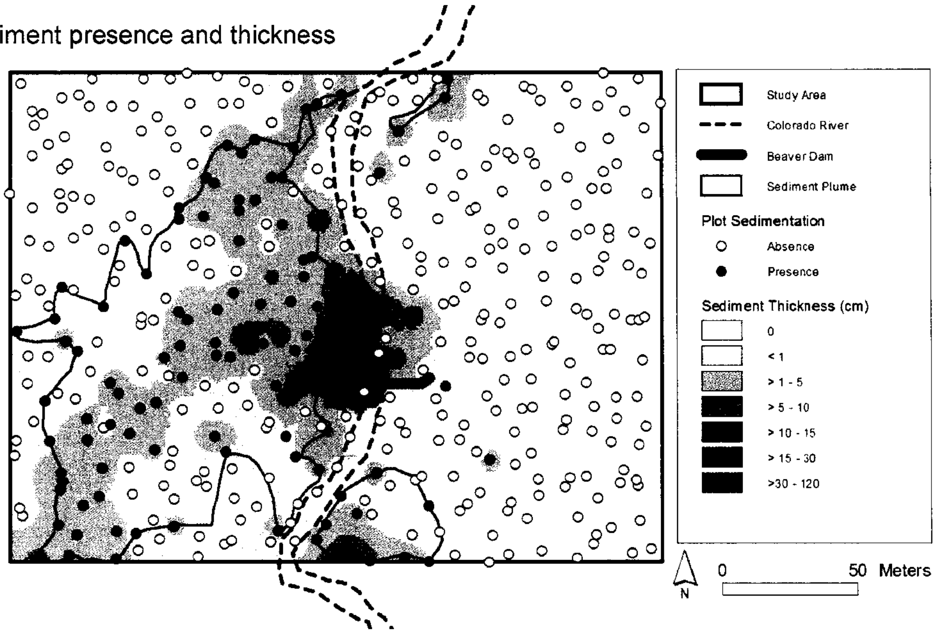
3.4 Results

3.4.1 Sediment deposition

Sediment was present in 28 % (112) of the 401 plots (Figure 3.2a) and averaged 6.0 cm thick (range 0-120 cm) where present. There were two main areas where sediment was deposited (Figure 3.2a). The 1.1-ha deposit west of the Colorado River contained ~750 m^3 of sediment and occurred where a surface slope of -0.02 m m^{-1} between the river and terrace allowed the majority of water to exit the river. Sediment accumulations were up to 120 cm thick behind the portion of the beaver dam that extended up the west side of the Colorado River. Accumulations were thinnest (< 1 cm) along the fringes of the deposit west of the Colorado River. There sediment deposited (0.2-ha deposit) downstream of the breached dam on a point bar and adjacent terrace east of the Colorado River accumulated on 29 May 2003 when the dam breached.

The sediment deposit west of the Colorado River had a texture that varied obliquely across the valley (Figure 3.2b). The percentage of fine sediments (silt plus clay) increased from 30 to 70 % as distance from the river channel along the water flow path increased, which suggests coarse sediments were deposited before fine sediments as river water was slowed by the in-channel beaver dam, beaver dams built on the adjacent terrace, and surface topography. The texture of the deposit east of the river was fairly homogeneous of approximately 50 % silt plus clay.

a) Sediment presence and thickness



b) Sediment texture (percent silt + clay)

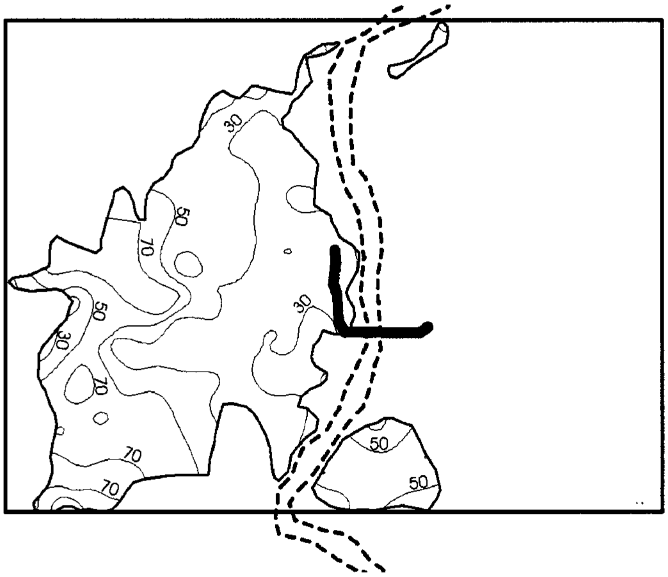


Figure 3.2 Presence of sediment (a) in 28 % of the 401 sampled plots and delineation of the three deposits of sediment within the study area. Also presented are kriged surfaces for sediment thickness (a) and texture (b; 20 % contour intervals). The sediment deposit west of the Colorado River occurred where a steeper hydraulic gradient (-0.02) between the river and riparian area allowed river water to exit the channel. The smaller sediment deposit south of the beaver dam and east of the river accumulated when the dam breached. The thickness of sediment decreased obliquely away from the beaver dam across the western sediment deposit and was relatively homogeneous east of the river. Sediment was generally coarser near the river channel and finer farther from it. These patterns indicate coarse sediments were deposited before fine sediments as river water was slowed by surface topography and beaver dams built on the terrace away from the river channel.

3.4.2 Deposits of C, N, and P

The mean concentration of sediment-associated TC was 24.1 g C kg^{-1} soil (SD = 16.2), TN was 1.5 g N kg^{-1} soil (SD = 1.0), and TP was 0.9 g P kg^{-1} soil (SD = 0.3). There were no significant relationships between sediment thickness and the quantities of TOC ($P = 1.000$), TN ($P = 1.000$), or TP ($P = 0.810$). However, there were significant (P < 0.001), positive, linear relationships between sediment texture (percent silt plus clay) and the quantities of TOC, TN, or TP, although they explained only 21, 37, and 36 % of the variation in the data. The correlation between sediment-associated nutrient deposition and sediment texture was further investigated by considering the role of organic matter as represented by the percentage of organic C in the deposited sediment. Strong positive relationships were found between the quantities of TN ($r^2 = 0.92$, $P < 0.001$) and TP ($r^2 = 0.64$, $P < 0.001$) deposited and the percentage of organic C in the deposited sediment, which indicates nutrients were primarily associated with organic matter in the sediment.

The C:N ratios in sediment averaged 20 (range 9 – 62, SD = 6.6), but 90 % of the plots had sediment C:N ratios less than 20. The C:P ratios in sediment averaged 27 (range 3 – 187, SD = 20.3). Taken together these results suggest mineralization is greater than immobilization for N and P in sediment. There were no spatial patterns of C:N or C:P ratios as these variables were not correlated to sediment texture or thickness ($P > 0.828$).

3.4.3 Nutrient availability

Resin bags were recovered from 40 of 112 plots with sediment and 141 of 289 plots without sediment; unfortunately, many missing bags were located in the sediment deposit west of the Colorado River. Resin-$N_{inorganic}$ (Resin-NO_3+NH_4) was not different (P = 0.157) for plots with (mean = 0.78 mg N bag^{-1}, SE = 0.21) and without (mean = 1.53 mg N bag^{-1}, SE = 0.48) sedimentation the summer following the failure of the beaver dam. Plots with sediment had two times less resin- PO_4 (mean = 0.05 mg P bag^{-1}, SE = 0.02, P = 0.013) than plots without sediment (mean = 0.12 mg P bag^{-1}, SE = 0.02). Resin bag nutrient content was not correlated with the quantity of sediment-associated nutrients ($P > 0.99$), sediment thickness ($P > 0.99$), or sediment texture ($P > 0.99$) for plots with sediment present, which indicates there were no spatial patterns.

3.4.4 Vegetation

Eighty-one vascular and one non-vascular plant species were found in the plots (Appendix A). The DCA depicted clear patterns of variation in the plant species assemblages (Figure 3.3a). Axes one (eigenvalue = 0.654) and two (eigenvalue = 0.437) explained 15 % of the cumulative variation in the species data (total inertia = 7.1). Axis one scores were correlated to hydrologic conditions in the post beaver occupation period (P = 0.074; r = -0.137) but were not correlated with any other of the explanatory ecological variables [hydrologic condition during the period of beaver occupation: r = -0.122, sediment thickness: r = -0.059, resin-$N_{inorganic}$: r = 0.028, resin-PO_4^-: r = -0.059] (Figure 3.3). Axis two scores were significantly correlated ($P < 0.001$) to hydrologic condition during the period of beaver occupation (r = 0.322) and sediment thickness (r = -0.233), but not to resin-$N_{inorganic}$ (r = -0.029) or resin-PO_4^- (r = 0.175) (Figure 3.3). Axis one therefore depicts a gradient from plots with deep water tables during the post beaver occupation period toward the left side of the biplot and plots with water tables seasonally near the soil surface toward the right. Axis two depicts a complex gradient from plots with thick sediment deposition and permanent standing water during the last three years of beaver occupation on the bottom of the biplot and plots without sediment deposition that had water levels that were deeper or seasonally near the soil surface during the beaver occupation toward the top.

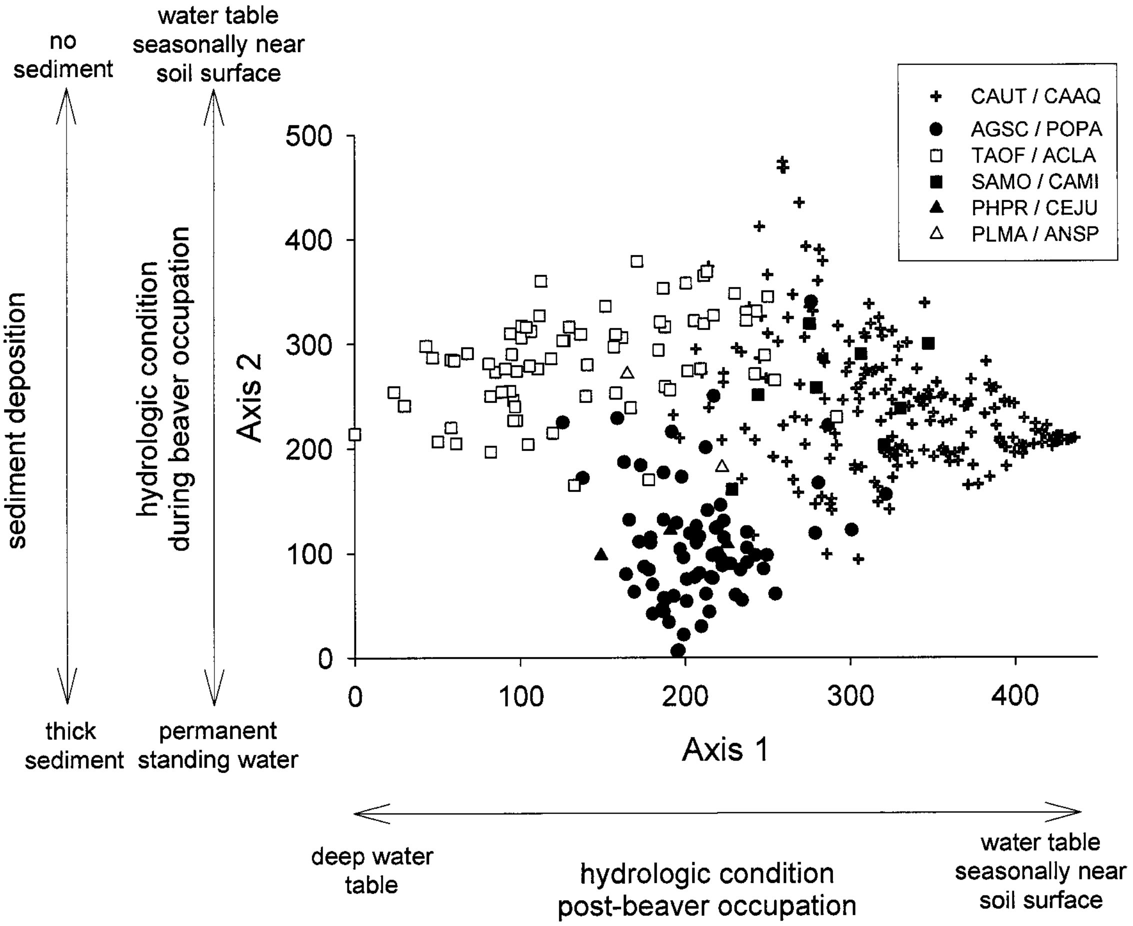


Figure 3.3 DCA ordination diagram for the plots that fall into each of the six plant communities identified through cluster analysis. The environmental variables influencing the plant species assemblages are shown for each axis.

Six different plant communities were identified using cluster analysis (Figures 3.3 and 3.4). Community 1 was composed of 224 plots with high cover of the sedges *Carex utriculata* (CAUT) and *C. aquatilis* (CAAQ) in areas of enhanced wetness due to seasonal inundation but lacked deep flooding during the period of beaver occupation. Only 27 % of the plots in community 1 had sediment deposited. Community 2 was composed of 73 plots with early successional species, including the indicator species *Agrostis scabra* (AGSC) and *Poa palustris* (POPA) in the area where water from the Colorado River had flowed across the terrace. These plots were deeply flooded during the beaver occupation and half were buried by sediment. Plots within communities one and two were located in areas where historical aerial photographs indicate a *Salix spp.* community occurred prior to the beaver occupation (Appendix C). Community 3 included 75 plots of upland relict species that were present prior to the beaver occupation. Indicator species for community 3 were *Taraxacum officinale* (TAOF), *Achillea lanulosa* (ACLA), *Deschampsia cespitosa* (DECE), and *Carex canescens* (CACA). Community 4 was composed of eight plots with plant species that survived permanent inundation during beaver occupation because they were on hummocks. Indicator species in community 4 were *Salix monticola* (SAMO), *Carex microptera* (CAMI) and *Polemonium caeruleum* (POCA). Community 5 was composed of three plots located in heavily disturbed areas that were very dry following the dam breach. Indicator species were two early successional grasses, *Phleum pratensis* (PHPR) and *Critesion jubatum* (CRJU). Community 6 was composed of two plots that had a hydrologic regime not affected by the beaver occupation. Indicator species in community 6 were the herbaceous dicots *Plantago major* (PLMA) and *Antennaria spp* (ANSP).

Figure 3.4 Aerial photograph of the study area showing six different plant communities defined through cluster analysis. Indicator plants for each cluster are presented as the first two letters from the genus and the first two letters of the species (refer to text and Appendix A for species names). The background aerial photograph was flown on 9 September 2001 and shows flooding at baseflow caused by the beaver dam (thick black line).

Willow seedlings were found in 49 (12 %) of the 393 plots, including 17 of the 112 plots where sediment was deposited. Most seedlings were either on the overbank deposit west of the river channel or in areas that had permanent standing water during the last three years that the beaver dam was intact. The deep flooding east of the river channel resulted in the death of nearly all vegetation that existed prior to the beaver dam in these areas and thus bare soil was exposed when the dam failed and the flood waters receded. Ninety percent of the willow seedling occurrences were in plots of the *C. utriculata* / *C. aquatilis* and *A. scabra* / *P. palustris* plant communities. Aspen seedlings were found in only 7 plots, and these were mainly on the sediment deposit west of the river. Further investigation near plots adjacent to the beaver dam revealed the presence of seedling clusters with tens of aspen in each. Four of the aspen seedling occurrences were in plots of the *A. scabra* / *P. palustris* community and the other two occurrences were in plots of the *C. utriculata* / *C. aquatilis* community.

3.5 Discussion

This study documents the process of beaver meadow formation on the floodplain and terrace of the Colorado River. An in-channel beaver dam triggered overbank flooding, killing vegetation in areas deeply flooded during the beaver occupation. Only vegetation on hummocks survived the deep flooding. Sediment accumulated on the floodplain and terrace west of the river along the main water flow path. The deposited sediment remained following the breach of the dam and is protected from future re-mobilization by overbank flood events because the deposition areas are disconnected from the river unless beavers build another dam that reconnects them. Areas east of the river did not accumulate sediment, but vegetation in these areas was drowned by the flooding. The drowned vegetation exposed mineral soil following the breach of the dam and de-watering of the study area. Bare deposited sediment and bare exposed soil was quickly colonized by the *C. utriculata* / *C. aquatilis* community on wet sites and the *A. scabra* / *P. palustris* community on dry sites, forming a beaver meadow. *Salix spp.* and *Populus tremuloides* seedlings were found throughout these two new communities, suggesting the beaver meadow may succeed to a shrub-carr plant community, potentially with isolated pockets of aspen trees.

3.5.1 Mechanism of landform generation

Beaver created a hydrologic connection between the Colorado River and the valley bottom (Westbrook et al., submitted) that permitted ~750 m^3 of sediment to accumulate in a fragmented pattern on the floodplain and terrace while the dam was active (August 1997 – May 2003). As the mean annual sediment yield for the Colorado River ranges between 15 and 6500 m^3 (assuming a bulk density of 2650 kg m^{-3}), the amount of beaver-deposited sediment on the floodplain and terrace is relatively large. Similar beaver-caused accumulation of sediment on floodplains has been found in the Spessart Uplands, Germany (John and Klein, 2003). The hydrologic connection we found means a > 200 year flood would be needed to achieve a stream stage similar to that produced by the 1.7-m height of our beaver dam (Westbrook et al., submitted). Sediment was transported across the floodplain by convective processes (Middelkoop and Asselman, 1998) in directions controlled by the pathways of floodwaters. Floodwaters moved from the river channel southwest across the valley bottom due to the slant of the valley in this direction (Braddock and Cole, 1990). Most sediment deposition occurred west of the river along the main dam-diverted flow path. Deposition of >1 m of sediment along the western flank of the beaver dam was likely the result of a large reduction in shear stress (Nicholas and Walling, 1998) as dams dissipate stream energy (Gurnell, 1998). The amount of sediment deposited did not decline with distance from the river, but did decline, albeit not exponentially, with lateral distance from the main dam-diverted flow vector across the floodplain and terrace. Thus are results are consistent with the observed decline in sediment accumulation from the main flow vector (Middelkoop and Asselman, 1998; Kronvang et al., 2002). The relatively uniform thickness with distance from the river channel may be attributed to the presence of off-channel beaver dams, which would have decreased the velocity of the moving water (Meentemeyer and Butler, 1999) and therefore been areas of reduced shear stress. At an even finer-scale, higher sediment deposition occurred in more sheltered locations on the floodplain and terrace, such as down-gradient of relict plant hummocks and in topographic depressions. The effect of the in-channel beaver dam on the deposition of sediment across the floodplain and terraces was more complex than that predicted from 'ideal' patterns of sediment transport by turbulent diffusion (Bridge, 2003). Our findings were more consistent with Jeffries et al. (2003) who showed that the combination of an in-channel coarse woody debris dam, vegetation and floodplain topography led to a spatially incoherent pattern of sediment deposition on a floodplain in England.

Beaver detained floodwaters on the terrace west of the river by building off-channel dams, which apparently slowed the movement of water across the ground surface enough so that sand, silt and clay was deposited. The considerably lower hydraulic gradient for water movement from the Colorado River toward the east side of the valley (Westbrook et al., submitted) resulted in ponding of water on the east terrace. Thus, river water probably did not have sufficient velocity to move sediment from the Colorado River onto the eastern floodplain and terrace and sediment instead settled within the channel where river water velocity was slowed upstream of the dam (Asselman and Middelkoop, 1995). The lack of beaver dams east of the river, aside from the easterly extension of the main dam onto the terrace, provides further support for this conjecture as beaver build dams to restrict the flow of water (Baker and Hill, 2003). The exposure of bare mineral soil following the breach of the dam and subsequent de-watering of the site created a new site in the valley where *Salix* spp. seedling could establish.

The rapid reductions in sand content of the sediment from the floodplain to the terrace and with increasing distance from the water flow path across the terrace surface are consistent with fluvial geomorphic theory (He and Walling, 1998). The sediment south of the dam and east of the river was deposited following the breach of the dam and probably originated from sediment stored in the pond. The percentage of silt plus clay across this sediment deposit was probably constant because it was mixed by river turbulence during its flushing from the beaver pond at deposited all at the same time.

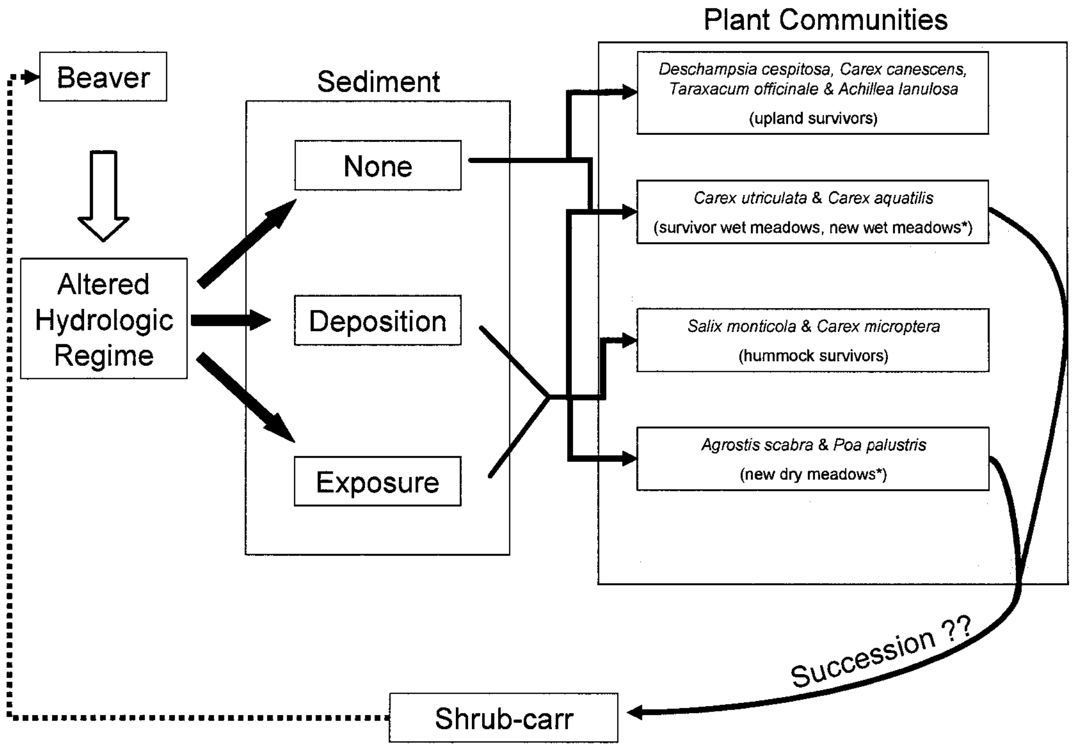
The total organic C, N, and P deposited in association with the sediment in the study area was approximately 102 kg C ha^{-1}, 7 kg N ha^{-1}, and 4 kg P ha^{-1}. Nutrients are transported with the sediment through transient sorption to mineral sediment grains (Triska et al., 1994) or as organo-complexes. The significant positive linear relationships of sediment percent silt plus clay with TOC, TN, and TP we found are consistent with the theory of preferential association of nutrients with fine-grained sediment particles, where fine-grained particles have greater surface area and thus higher cation exchange capacity and microbial colonization capacity (Walling and He, 1994; Songster-Alpin and Klotz, 1995; Steiger and Gurnell, 2002). However, sediment texture explained relatively little of the variation (< 37 %) in nutrient content. This may be because the majority of the sediment samples had high sand contents. The variation in nutrient content was better explained by the percent TOC, suggesting that the amount of deposited organic matter, rather than the amount of mineral sediment, controlled sediment nutrient status. This contrasts with the findings of Steiger and Gurnell (2002), who showed that the texture of deposited sediment controlled the amount of deposited TOC and total organic N.

Sediment C:N and C:P ratios were generally < 20 and < 200, which should promote net N and P mineralization (Paul and Clark, 1996). Drying of sediment after beaver dams are breached and floodplain water levels decline can result in sequestration of bio-available nitrogen and phosphorus. These nutrients may be released upon re-wetting (Scholtz et al., 2002) by streamflow, rainfall, or snowmelt events. While the precipitation records show near average rainfall throughout the two summers following the beaver dam breach, nutrient availability was significantly lower in the newly-deposited sediments than in the soils present prior to the beaver disturbance. Pinay and Naiman (1991) found enhanced nitrogen cycling and availability due to rapid shifts in the hydrologic condition adjacent to beaver-flooded areas. The soils in areas adjacent to those permanently flooded during the beaver occupation had a relatively dynamic hydrologic regime as they had water tables that were high during the snowmelt period and then declined over the summer, suggesting an increase in nutrient availability in plots that did not receive sediment. In addition, plots where sediment was deposited may have had relatively lower nutrient availability because of the strong relationships between percent TOC and sediment nutrient content. The organic matter may have been fairly recalcitrant as the organic matter was often conifer needles; this would slow decomposition and associated nutrient release (Trumbore, 2000). These data suggest that the beaver-created landforms in our study were unlike those reported for boreal forests (Naiman and Melillo, 1984; Pinay and Naiman, 1991), as they had lower nutrient availability than surrounding areas where no sediment was deposited.

3.5.2 Vegetation patterns and beaver meadow creation

The plant community composition following beaver abandonment was spatially heterogeneous. The plant community composition was not influenced by soil nutrient availability as has been found in other studies (Steed et al., 2002; Wassen et al., 2002; Wright et al., 2002). Instead, the plant community composition was found to be controlled by the pattern of sedimentation and the hydrologic regime during and following beaver occupation. These results contrast with those from studies in low-energy riverine environments, where beaver-created patches increase species richness at a landscape scale but are themselves fairly homogeneous units (Wright et al., 2002). The observed heterogeneity in this young environment was similar to that observed in older beaver meadows found in eastern temperate riverine environments that developed varied topography due to sediment erosion and formed a varied plant community from a sedge-dominated community over time (McMaster and McMaster, 2001).

A simple conceptual model of the landforms and plant communities present following beaver occupation and the potential trajectories or fates of these plant communities was constructed (Figure 3.5). Plant communities in areas that had no bare sediment following the beaver occupation were either: (1) relict upland plants that were not killed during the beaver occupation because water levels remained below the ground surface; or (2) newly formed wet meadows dominated by *C. utriculata* / *C. aquatilis* because the plots were periodically inundated during the beaver occupation. The dominant vegetation in the areas flooded by the beaver dam can be seen on the 1969 and 1987 air photos, confirming my classifications of relict plant communities (Appendix C). Areas with sediment deposition were classified into three plant communities. Some plants survived the deep flooding during the beaver occupation because they were located on hummocks. Other plant communities colonized the bare sediment that reflected wet meadow or dry meadow conditions, depending on the hydrologic regime following the beaver occupation. Where deep flooding during the beaver occupation killed existing vegetation, bare mineral sediment was exposed following the dam breach and was colonized by wet or dry meadow plant communities, depending on the post-beaver occupation hydrologic regime. Also, some plant communities east of the river survived the deep flooding on hummocks.



* Frequent occurrences of *Salix spp.* & *Populus tremuloides* seedlings

Figure 3.5 Conceptualization of the direct influence of beaver activities on hydrologic processes, which indirectly alters sediment deposition dynamics and vegetation patterns in high-energy riverine environments.

The resultant heterogeneity requires an expansion of the term "beaver meadow" to include those patches created by beaver dam-building activities on floodplains and terraces.

Plants that colonized bare sediment will influence the probable successional trajectory of the study area, as will future environmental conditions (Figure 3.5). The plots that had wet or dry meadow vegetation in the summer following the beaver dam breach were those with the highest occurrences of *Salix spp.* and *Populus tremuloides* seedlings. *Salix* species favor disturbed habitats and survival rates increase rapidly as seedlings age and become more dependent on groundwater rather than soil moisture (Karrenberg et al., 2002). Historic air photos show that shrub-carr plant communities are common throughout the upper Colorado River valley. Thus plots with *Salix* seedlings have the potential to succeed from wet or dry meadow to a shrub-carr community if the seedlings survive, grow and flourish. Succession of the wet and dry meadows to a shrub-carr community would make the area conducive to beaver reoccupation as willow stems are their primary source of food and building material in the valley (Baker and Hill, 2003). In the summer of 2005 there were both *Salix spp.* and *Populus tremuloides* seedlings in the plots that had seedlings in 2004, but the long-term fate of these seedlings is uncertain. The upper Colorado River valley is intensely browsed by elk (*Cervus elaphus*) and moose *(Alces alces*), which appears to be causing a decline in the vigor of shrub community. Elk browsing has drastically reduced the vigor of *Salix* and other shrubs in other valleys within Rocky Mountain National Park (Peinetti et al., 2002; Baker et al., 2005, Gage and Cooper, 2005). Intense ungulate herbivory may drive the former beaver-engineered shrub-carr community towards relatively dry meadows that persist as sedge- or grass-dominated patches that are unable to support beaver. Thus, the successional pathways for particular plots will likely be multidirectional and non-linear, as has been observed by other researchers (Remillard et al., 1987).

3.5.3 Beaver-driven valley formation

This study analyzed the effects of a beaver dam typical of the types of dams that form in the study region on the processes leading to beaver meadow formation in a high-energy environment. The beaver population in the study valley was only 5% of the 600 beaver that were estimated to have been present in 1940 (Packard, 1947; Mitchell et al., 1999). Before 1940, beaver may have been even more abundant, as fur trapping decimated populations after European settlement (Seton, 1929). The results suggest abundant beaver would have largely structured valley formation as abundant beaver are key drivers of valley development throughout North America, where streams are small enough to be dammed. The cycle of beaver colonization and abandonment of dams over time could lead to layering of beaver-created patches on top of one another throughout the valley's floodplain and terrace. Such layering supports Ruedemann and Schoonmaker's (1938) hypothesis of beaver-driven valley formation; although by a different process than that documented for low-energy riverine environments (Meentemeyer and Butler, 1999; Bigler et al., 2001).

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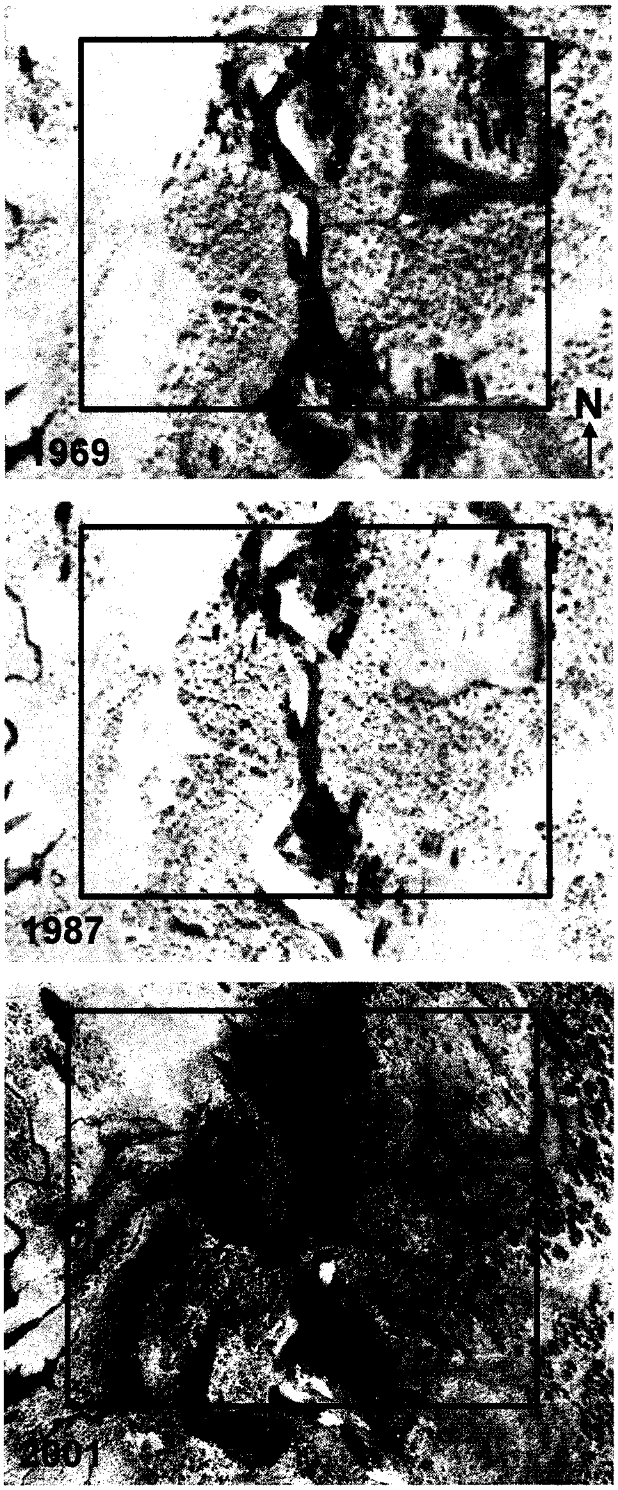
Appendix 3A Species scientific names and codes.

Code	Name
Trees and Shrubs	
ABBI	*Abies bifolia*
ALIN	*Alnus incana ssp. tenuifolia*
BEGL	*Betula glandulosa*
PICO	*Pinus contorta*
PIEN	*Picea engelmannii*
POTR	*Populus tremuloides*
SADR	*Salix drummondiana*
SAGE	*Salix geyeriana*
SALA	*Salix lasiandra*
SAMO	*Salix monticola*
SAPA	*Salix planifolia*
SASP	*Salix spp.* seedling
SAWO	*Salix wofii*
Sedges and Rushes	
CAAQ	*Carex aquatilis*
CAAT	*Carex athrostachya*
CACA	*Carex canescens*
CAMI	*Carex microptera*
CAUT	*Carex utriculata*
CAVE	*Carex vesicaria*
JUAR	*Juncus arcticus*
JUTR	*Juncus tracyi*
Grasses	
AGSC	*Agrostis scabra*
ALPR	*Alopecurus pratensis*
BESY	*Beckmannia syzigachne*
BRCI	*Bromus ciliatus*
CAIN	*Calamagrostis inexpansa*
CALC	*Calamagrostis canadensis*
CRBR	*Critesion brachyantherum*
CRJU	*Critesion jubatum*
DECE	*Deschampsia cespitosa*
ELTR	*Elymus trachycaulus*
GLST	*Glyceria striata*
PHAL	*Phleum alpinum*
PHPR	*Phleum pratense*
POPA	*Poa palustris*
POPR	*Poa pratensis*

Code	Name
Herbaceous Moncots and Dicots	
ACLA	*Achillea lanulosa*
ACRU	*Actea rubra*
ANSE	*Androsace septentrionalis*
ANSP	*Antennaria sp.*
ASAL	*Astragalus alpinus*
ASSI	*Aster sibiricus*
CEAR	*Cerastium arvensis*
CHDA	*Chamerion danielsii*
CISC	*Cirsium scariosum*
COSC	*Conioselinum scopulorum*
DAFL	*Dasiphora floribunda*
DESP	*Descurainia spp.*
EPCI	*Epilobium ciliatum*
EPHO	*Epilobium hornemannii*
EQAR	*Equisetum arvensis*
FRVE	*Fragaria vesca*
GABO	*Gallium boreale*
GATR	*Galium trifidum*
GEMA	*Geum macrophyllum*
GERI	*Geranium richardsonii*
GNUL	*Gnaphalium uliginosum*
HELA	*Heracleum lanatum*
IRVI	*Iris virginica*
MART	*Martimum sp.*
MECI	*Mertensia ciliata*
OXFE	*Oxypolis fendleri*
PLMA	*Plantago major*
POCA	*Polemonium caeruleum*
PODO	*Polygonum douglasii*
POPU	*Potentilla pulcherrima*
ROPA	*Rorippa palustris*
RUMA	*Rumex maritimus*
RUSA	*Rumex salicifolius ssp. fueginus*
SMST	*Smilacina stellatum*
SOLI	*Solidago sp.*
SPMA	*Spergularia marina*
STNE	*Stipa nelsonii*
TAOF	*Taraxacum officinale*
THFE	*Thalictrum fendleri*
TRRE	*Trifolium repens*
UNKN	unknown
VEAM	*Veronica americana*
VIOL	*Viola sp.*
Non-vasular	
DRSP	*Drepanocladus spp.*

Appendix 3B Photograph of the study area taken after the dam breach (23 July 2003) shows areas where sediment was deposited (far bottom right of the study area) and the different plant communities.

Appendix 3C Historic photographs illustrating the vegetation communities throughout the study area (black box) prior to the beaver occupation (1969, 1987) and during the beaver occupation (2001). Deep flooding on the floodplain and terrace because of the beaver dam can be seen in the 2001 photo, particularly west of the Colorado River.



4. BEAVER: BEYOND THE PONDS

4.1 Introduction

Organisms that can create, modify, and maintain their habitat directly or indirectly by changing the availability of biotic or abiotic resources are often called ecosystem engineers (Jones et al., 1994; Brown, 1995). Ecosystem engineers have a large influence on the flow of materials and energy in ecosystems throughout North America (Butler, 1995; Jones et al., 1997). Examples include alligators (*Alligator mississippiensis*) that provide refuge for a variety of bird species by creating wallows in Everglades National Park (Craighead, 1968), prairie dogs (*Cynomys* spp.) that alter soil nutrient cycling in short and mixed grass prairie by burrowing and creating soil mounds (Whicker and Detling, 1988), *Sphagnum* spp. mosses in northern or boreal bogs that control peat formation and soil water nutrient status (van Breemen, 1995), and phytoplankton that regulate light interception and temperature regimes in freshwater lakes (Mazumder et al., 1990). In aquatic and semi-aquatic environments of North America, beaver (*Castor canadensis*) are the key ecosystem engineers (Gurney and Lawton, 1996) that affect landscape structure and dynamics at a level rivaled only by humans (Butler, 1995).

Descriptions of beaver natural history and effects on ecological processes were plentiful in the late 1800s and early 1900s (e.g. Mills, 1913; Dugmore, 1914). Some of the concepts – such as beaver create and maintain riparian wetlands, beaver ponds function as efficient sediment traps that eventually become meadows, and below beaver dams there is reduced erosion because the dam reduces stream velocity – were generally accepted and became grounded in the ecological literature without rigorous quantitative testing (Gurnell, 1998; Meentemeyer and Butler, 1999). Only in the latter half of the

1900s did researchers begin to test concepts of beaver effects on physical and biological processes in ecosystems (e.g. Wilde et al., 1950; Barnes and Dibble, 1986; Naiman et al., 1986; Butler and Malanson, 1995). Research has focused on the influence of beaver on ecosystem processes, primarily on first and second order rivers, and the effects of beaver dams and the upstream ponds on local water tables, sediment trapping, soil biogeochemical cycling, and vegetation succession following abandonment (Naiman et al., 1988; Butler, 1995; Gurnell, 1998). However, beaver that live in rivers of any size also can have significant impacts on landscape processes, including groundwater or precipitation fed peatlands, through felling of trees for food and building of dams, dens, lodges, canals, and food caches, diversion of streams across floodplains, and valley development. This paper looks at and beyond the beaver ponds on small rivers, examining the hydrologic, geomorphic, biogeochemical, and ecological processes that beaver affect throughout landscapes.

4.2 History of beaver in North America

The genus *Castor* originated in the Pleistocene (1.8 million years BP) or the late Tertiary (2.4 million years BP) (Baker and Hill, 2003). The formation and melting of Pleistocene ice sheets in North America probably affected beaver evolution and abundance during this period. The Paleo-Indians who migrated to the continent approximately 18,000 to 8,000 years BP likely interacted with beaver, however their effects on abundance are not well known. Prior to the settlement of Europeans in North America, the beaver population was estimated to be between 60 and 400 million (Seton, 1929). Their range was estimated to cover ~15 million km^2 and included all of North

America other than the North Slope of Alaska, northern Nunavut, southern California, south-central Florida, central and southern Nevada, and the Texas Panhandle (Jenkins and Busher, 1979; Baker and Hill, 2003). The arrival of Europeans initiated the systematic elimination of beaver from much of its range, largely to supply pelts for felt hats in Europe (Figure 1; Bryce, 1904). Large fur-trading companies, such as the Hudson Bay Company and the Rocky Mountain Fur Trading Company, employed both European and First Nations people to trap beaver in north-eastern Canada and the eastern U.S. starting in the early 1600s through the 1700s (Baker and Hill, 2003). Continued demand for felt hats and the decline of beaver in the East persuaded trappers to move west during the mid-1700s to mid-1800s, which helped encourage Caucasian settlement of the western states (Cline, 1974 referenced in Naiman et al., 1988). Excessive trapping led to a near extirpation of the beaver population by 1900 throughout North America. At the beginning of the twentieth century the direction of fashion moved away from furs and toward silk (Marston, 1994). Public concerns about the large declines in beaver and other fur-bearing animals led to the implementation of trapping regulations. The population recovery that ensued was facilitated by reintroduction efforts which peaked in the 1950s (Baker and Hill, 2003). While beaver are now present throughout most of their former range, they are estimated to have re-populated at a density of about 10 %, or between 6 and 12 million individuals, due to a concomitant loss of habitat through conversion of wetlands to drylands (Naiman et al., 1988). Beaver populations have not thrived where there is excessive competition with other herbivores for riparian shrubs and trees, such as some parks in the Rocky Mountains (Meentemeyer and Butler, 1995; Nietvelt, 2001; Baker et al., 2005).

Figure 4.1 Historic examples of human use of beaver. A) An unidentified Osage Native American wearing a traditional beaver bandeau with feathers c. 1890. *Denver Public Library, Western History Collection, Hutton, X-32593.* B) Colin Fraser, a trader, sorts fox, beaver, mink and other furs at Fort Chipweyan, a trading post in northern Alberta c. 1895. *Library and Archives Canada, Brown, C-001229.*

4.3 Hydrologic processes

Hydrologic processes affected by beaver include streamflow regulation, valley flooding, and groundwater-surface water interactions. The main influence of beaver on hydrologic processes is through dam construction, which can change the amount of water flowing downstream (Figure 4.2). Discharge and velocity are often reduced below beaver dams and the magnitude of these effects is a function of dam size, age, condition, and storage capacity of the upstream pond (Meentemeyer and Butler, 1999). Younger dams are less efficient in reducing streamflow velocity than older dams because they are initially porous and then leak less as sediment accumulates (Woo and Waddington, 1990). However, in the western US where many streams are deeply incised, streamflow regulation may not occur to a great extent as beaver may not be able to build a dam high enough to extensively pond water (Apple et al., 1985). Storage of water in beaver ponds and on floodplains can increase the annual residence time of stream water (Devito and Dillon, 1993), enhance evaporation rates (Woo and Waddington, 1990; Burns and McDonnell, 1998), and increase the probability of overbank flooding with a given stream discharge (Westbrook et al., submitted). In boreal forests or other areas of low relief, beaver dams can pond water high enough to divert it over the watershed divide and into another basin (Dugmore, 1914; Woo and Waddington, 1990).

Beaver also controls flooding by digging canals and building dams on floodplains and terraces in order to expand their habitats (Figure 4.2; Naiman et al., 1988; Baker and Hill, 2003). The areal extent of flooding created by beaver dams is controlled by a combination of dam height relative to river bank height, the width of the dam, and the elevation of the valley relative to the height of the dam. The surface water storage capacity upstream of dams in confined valleys may be large (Neff, 1957; Naiman et al., 1988) while in an unconfined valley storage of water upstream of dams may be relatively small compared to downstream flooding if dams do not extend across the entire valley width (Westbrook et al., submitted). In unconfined valleys a large portion of the volume of the stream may be diverted onto the floodplain (Woods, 2000), further spread across the floodplain and terraces in a braided river fashion by a series of off-channel dams, ponds and canals (Westbrook et al., submitted), and eventually returned to the stream tens to hundreds of meters downstream (Woo and Waddington, 1990; Lowry and Beschta, 1994).

Ponding increases the water pressure behind a beaver dam, which can increase the hydrologic interaction of the stream with its bed. Similar to man-made dams, surface water is driven into the stream bed behind the dam, flows as hyporheic water under the dam, and re-emerges as surface water downstream (White, 1990; Triska et al., 2000). Ponding of stream water behind beaver dams also increases the pressure differences, or hydraulic gradient, between the stream and the valley water table and enhances infiltration of stream water into the near stream aquifer (Lowry and Beschta, 1994). Enhanced infiltration can increase groundwater levels near the pond and if it occurs over a large enough area, can lead to substantially greater groundwater storage in a valley (Woo and Waddington, 1990; Westbrook et al., submitted). In valleys where the principal direction of groundwater flow is down-valley, enhanced infiltration into river banks can cause a local change in the direction of groundwater flow toward the valley center, and groundwater will ultimately loop around the dam (Lowry and Beschta, 1994; Westbrook et al., submitted). The scale of this looping can vary from tens to several hundreds of meters. The location of a dam in relation to a valley's main direction of groundwater flow and valley confinement also may determine whether beaver dams affect patterns of groundwater flow. For example, dams built across a channel with a geometry that is parallel to the direction of groundwater flow will have little effect on flow patterns but can have large effects on the magnitude of flow because of the increased hydraulic gradient between the stream and riparian area (Westbrook et al., submitted). Also, there are water level differences and thus pressure differences above and below dams in oxbows, abandoned channels or in peatlands (Jeglum, 1975), but we know very little how dams in these types of landscape settings affect surface water-groundwater interactions in valleys.

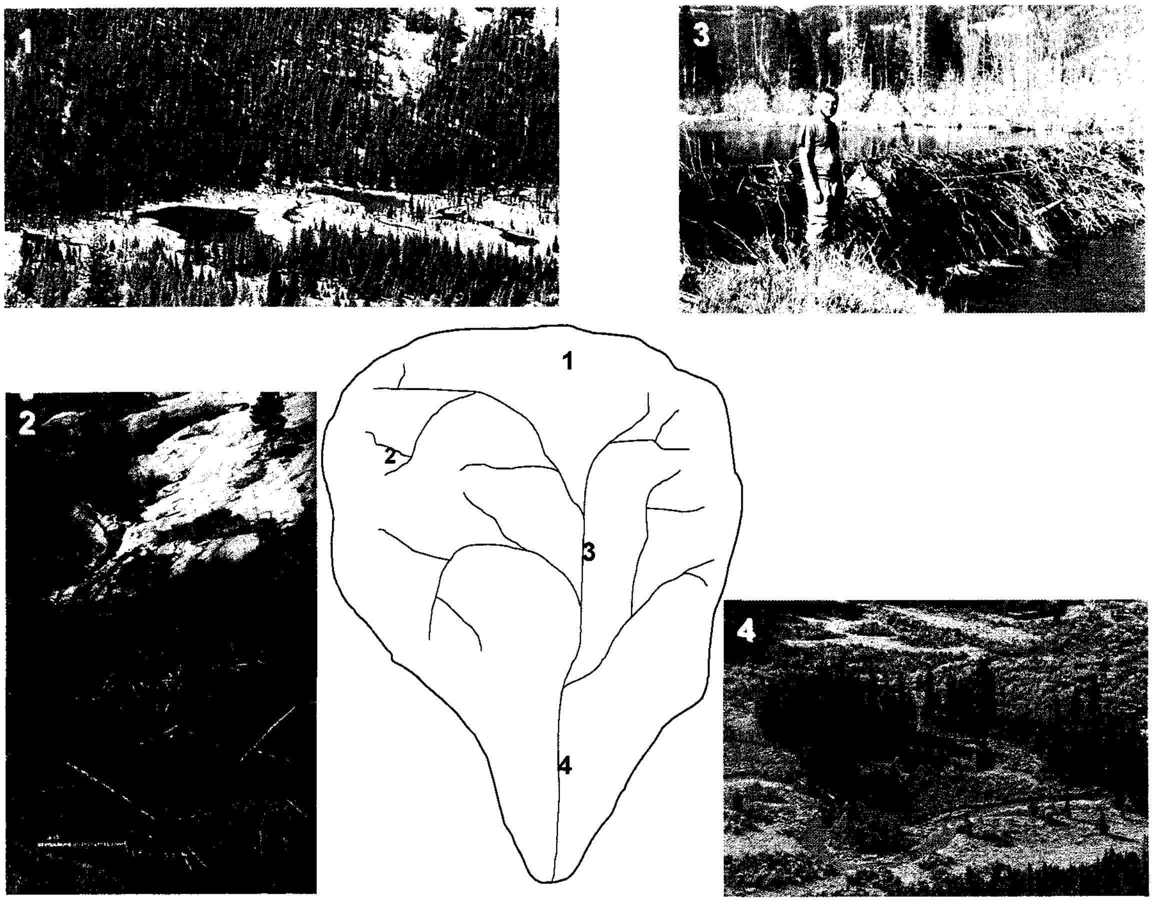


Figure 4.2 Beaver affect hydrologic processes throughout watersheds. (1) Photograph of a series of beaver ponds and dams in a groundwater-fed peatland. (2) Beaver dams built in steep, confined valleys where upstream ponds are the main hydrologic features (source: *Denver Public Library, Western History Collection, Rose & Hopkins, H-168*). (3) Beaver ponds upstream of dams build on rivers where stream power and discharge are near the limits of where beaver can successfully build dams have relatively small hydrologic effects compared with alterations to downstream hydrologic processes. (4) Beaver can also affect hydrologic processes on the floodplains of larger rivers by building dams (arrow) in oxbows.

4.4 Geomorphic processes

Beaver have a substantial impact on valley geomorphic processes through sediment trapping, sediment re-distribution, and alterations to channel morphology. The most well-known effect of beaver on geomorphic processes is sediment trapping behind dams. Sediment accumulates in beaver ponds as they age (Meentemeyer and Butler, 1999). Butler and Malanson (2005) estimated that approximately 4 billion m^3 of sediment is currently trapped in beaver ponds; prior to European settlement of North America the volume of sediment trapped was 7 to 125 billion m^3. The total amount of sediment accumulated in ponds is also related to stream order, surficial geology and upstream bank erodibility (Butler and Malanson, 2005). Sediment also can accumulate on floodplains and terraces when beaver dams temporarily or permanently divert stream water across wide valleys (Chapter 3; John and Klein, 2003; Cooper et al., in press). The processes of trapping sediment behind dams and on floodplains and terraces may lead to valley development or the development of peatlands or other organic-rich landforms over time. Ruedemann and Schoonmaker (1938) hypothesized that since the last glaciation, layering of drained sediment-filled beaver ponds throughout valleys has contributed substantially to valley formation by accumulating successive horizontal plains of sediment. The cycle of beaver colonization and abandonment of dams over time could lead to layering of sediment-filled beaver ponds (Meentemeyer and Butler, 1999; Bigler et al., 2001) and landforms created by dam-diversion of water and sediment onto floodplains and terraces (Chapter 3; John and Klein, 2003). Archeological evidence suggests that the deposition of silty sediment altered the hydrology of an area in England enough for peatland inception and paludification to occur (Wells et al., 2000). Further, palsas, which are circular or oval organic-rich permafrost mounds, were found to only redevelop after beaver dam breach as permafrost aggrades in the newly exposed sediment, although the process leading to their formation is not yet clear (Lewkowicz and Coultish, 2004).

Beaver can redistribute sediment in the landscape by building bank dens, canals and slides. They excavate sediment by constructing canals and bank burrows, which can de-stabilize stream banks, but sediment loss has rarely been quantified (Meentemeyer et al., 1998). Beaver-driven sediment storage behind dams and on floodplains and terraces in higher parts of watersheds results in a concomitant decrease in downstream turbidity and sediment yield from watersheds (Meentemeyer et al., 1998) – sediment additions to streams through beaver excavation of canals and bank burrows only partially offset these effects. Beaver may also redistribute sediment at a local scale as they build dams in boreal and montane peatlands as they excavate the peat to enlarge natural moats or small natural flowages and then dam the flowing water (Rebertus, 1986). There have been no estimates of the quantity of peat removed to form ponds and associated canals in peatlands or whether sedimentation occurs in peatland beaver ponds. As peatlands are rarely directly connected to the watershed's stream network, landscape scale effects are unlikely.

Beaver dam-building may alter stream morphology and channel development. Dams create sharp boundaries in the stream system, creating a stair-step profile (Naiman et al., 1988) that can be magnified when a sequence of dams is present. Beaver dam removal temporarily increases stream power and may trigger channel entrenchment, particularly when the failure of an upstream dam causes a water and sediment surge that blows out downstream dams (DeBano and Schmidt, 1989; Marston, 1994; Hillman, 1998). Channel evulsion may occur in valleys where beaver dams divert stream water out of the stream and across the floodplain and terrace if the diversion downcuts enough to form a permanent route (Cooper et al., in press).

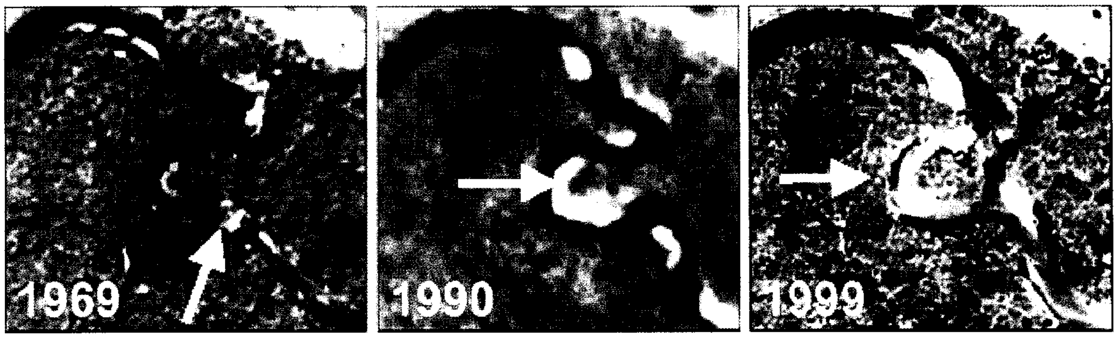


Figure 4.3 Comparative air photos from Moraine Park in Rocky Mountain National Park demonstrate effects that beaver can have on geomorphic processes. Air photos illustrate the identical river reach as a beaver pond (1969), point bar (1990), and abandoned channel (1999). Arrows show location of beaver dam (1969), point bar (1990), and abandoned channel (1999) (Cooper et al., in press).

4.5 Stream water biogeochemical dynamics

There has been extensive research on the role of beaver in the alteration of stream chemistry because of the potential impact on downstream productivity. This work has occurred largely in the eastern U.S. and Canadian Shield, and little is known about how beaver dams impact stream chemistry in the other parts of North America. Stream pH is often higher below dams (Smith et al., 1991), suggesting that ponds can alter the biogeochemical cycling of stream water (Cirmo and Driscoll, 1993). Beaver ponds tend to be a sink for nitrate, sulfate, ionic forms of aluminum, and dissolved oxygen, and a source of dissolved organic carbon, iron, manganese, and ammonium (Maret et al., 1987; Smith et al., 1991; Cirmo and Driscoll, 1993). The sink/source dynamics of beaver ponds are controlled by the hydraulic residence time, which drives the interaction time of stream water with bed sediments. There are marked seasonal variations in water chemistry, as beaver dams can attenuate streamflow during summer low flow periods but have little influence of streamflow during high runoff periods such as snowmelt or rain events (Cirmo and Driscoll, 1993; Devito and Dillon, 1993). Also, there is a greater potential for biotic assimilation of nutrients during the summer than winter (Devito and Dillon, 1993). Trapping of sediment upstream of dams may increase nitrogen and phosphorus concentrations in stream channel sediments by 9 to 1000 times compared to riffles (Naiman and Melillo, 1984; Francis et al., 1985; Maret et al., 1987). A greater volume of sediment in beaver ponds increases microbial activity of the stream reach (Songster-Alpin and Klotz, 1995), whereas the degree of anoxia in the pond sediment controls biogeochemical cycling and ultimately may enhance the productivity of a stream (Dahm et al., 1987; Klotz, 1998).

Considerably less is known about how stream chemistry is affected by beaver building in-channel dams that raise water above the river banks and move water around dams and onto floodplains. This may cause flushing of nutrients from riparian soils, which once they enter streams, can enhance in-stream productivity. Transport of newly-mobilized nutrients from floodplain and terrace soils to the stream may depend on the flowpath that stream water takes and the interaction time of stream water with riparian plants, periphyton on floodplains, and sediment. I am currently quantifying the effects of flow diversion across valleys on stream water chemistry. I measured dissolved inorganic nitrogen concentrations along the floodplain and terrace flowpaths created by the Upper Dam discussed in Chapter 2 during the summer in 2004. Preliminary results show higher dissolved organic nitrogen (DON) along the floodplain/terrace flowpath, suggesting flushing of DON from riparian soils to the Colorado River (Figure 4.4). However, the river water chemistry does not reflect this input, probably because of the small volume of this water input relative to the Colorado River volume at the point of entry.

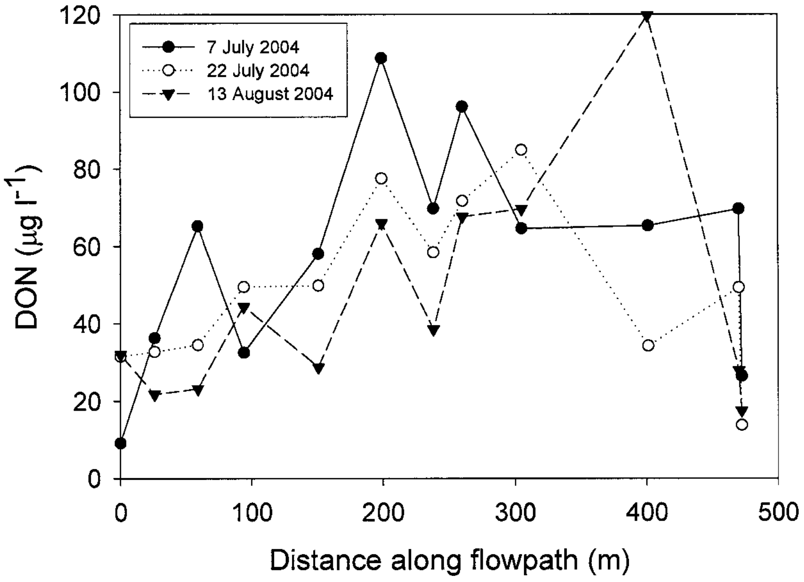


Figure 4.4 Change in dissolved organic nitrogen (DON) concentration along the beaver-created flowpath of Colorado River water from the channel, across the valley surface, and eventually back to the river 472 m downstream of the dam for three dates in the summer of 2004. Movement of water across the valley generally increases DON concentrations two-to three-fold, suggesting DON is flushed from riparian soils to the river.

4.6 Vegetation dynamics

Beaver can affect vegetation dynamics through selective cutting of wood for food and building materials, creating dams and ponds on streams that infill with sediment over time, and by flooding floodplains. Beaver are herbivorous, semi-aquatic rodents that selectively forage on trees and shrubs, preferring aspen, cottonwoods, willows, birch, and poplar where available (Baker and Hill, 2003). Beaver cut at least a metric ton of wood a year for food and building materials within 100 m of their ponds in northern areas (Johnston and Naiman, 1987). Beaver may thus alter the riparian plant community structure of the small streams they dam. For example, sapling recruitment of non-preferred species has been shown to be positively related to forage intensity and the total stem abundance, while basal area of preferred species has been negatively related to forage intensity in a boreal region of Ontario (Donker and Fryxell, 2000). Selective foraging on early- and mid-successional species can alter succession such that any plant species can become established at any time, or all species can establish at the same time (Barnes and Dibble, 1986). Others have shown that selective foraging increases light availability, which can promote growth of non-preferred species or can reverse succession by optimizing for growth of late-successional species (Naiman et al., 1988; Johnson and Naiman, 1990; Suzuki and McComb, 1998).

Effects of selective foraging may not be as great on willow species compared to other woody plants, as the number of regenerated willow stems is proportionate to the number cut by beaver (Kindschy, 1989). A model of beaver foraging has shown that a family of six beaver can be indefinitely sustained by a 4 ha willow community in the Rocky Mountains (Raul Peinetti, unpublished data). However, recovery of willow following beaver cutting may be suppressed in areas where there is intense ungulate herbivory (Baker et al., 2005), or deep water tables (Wolf, 2004). Less is known about the effects of selective foraging behavior in peatlands and large rivers. Beaver living in peatlands have been shown to clearcut transportation corridors through undesirable shrubs such as leatherleaf (*Chamaedaphne calyculata*) to access areas with preferred trees and shrubs from their ponds (Mitchell and Niering, 1993), but the effects of beaver foraging on peatland plant community composition remains largely unknown. Recent work on large rivers, where beaver do not build dams, has shown that the distance of trees from water and the tree size are important factors controlling cutting rates (Breck et al., 2002). Cottonwood (*Populus fremontii*) trees near large rivers are foraged more than those farther away and this greater cutting pressure closer to rivers maintain the cottonwood in a shrub-like architecture (McGinley and Whitham, 1985).

The hydrologic regime of beaver-dammed streams drowns plants upstream of dams. Flooding can kill woody vegetation in one or two growing seasons, athough the inundation tolerance of many willow species is longer (Nummi, 1989). Ponds fill in with sediment over time, drain, are rapidly colonized by plants, and eventually develop into beaver meadows (Johnston and Naiman, 1987; Meentemeyer and Butler, 1999). Beaver meadows are usually open meadows dominated by grasses or sedges depending primarily on the local moisture regime (Ives, 1942; McMaster and McMaster, 2001; Wright et al., 2002; Cooper et al., in press). Few beaver meadows ever succeed to riparian conifer forest and instead follow multidirectional and nonlinear successional pathways, persisting for decades to centuries on the landscape as patches dominated initially by emergent or herbaceous vegetation and potentially shubby vegetation over time (Neff, 1957; Barnes and Dibble, 1988; Remillard et al., 1987; Naiman et al., 1988; Terwilliger and Pastor, 1999). Patches may eventually be re-colonized by beaver within 10 to 30 years if they prove to be suitable habitat (Remillard et al., 1987). Beaver-caused changes in community composition at the scale of patches can increase landscape-scale plant species richness if the landscape was forested prior to beaver invasion and if beaver patches do not dominate the landscape (Wright et al., 2003).

Outside of streams, vegetation on floodplains, terraces, near oxbows, and in peatlands may change due to beaver alterations of the local hydrologic regime. Beaver dam-building activities in streams result in the transformation of terrestrial to wetland and lotic to lentic ecosystems (Pinay and Naiman, 1991), which can cause the vegetation on floodplains and terraces to change to plants adapted for wetter conditions (Townsend and Butler, 1996; Ray et al., 2001). In higher-energy environments beaver meadows can be located on floodplains and terraces (Chapter 3) where new vegetation may establish on bare sediment after the sites drain (Cooper et al., in press). Plant communities that colonize beaver meadows in these environments may be more spatially heterogeneous than meadows that develop from sediment-filled beaver ponds because of the variable pattern of sediment accumulation and water availability on the landscape (Chapter 3). Beaver ponds in peatlands can also change successional pathways. Plant communities remain relatively unchanged where the peat surface has the ability to float up and down with changes in water level (Naiman et al., 1988; Mitchell and Niering, 1993). Where surfaces are stable however, beaver ponds have been shown to affect vegetation patterns by increasing the abundance of nutrient-rich species (Mitchell and Niering, 1993) or by altering geomorphic conditions (Wallbridge, 1994), which affect primary succession (Rebertus, 1986).

4.7 Conclusions

Beaver ponds on streams are the main hydrologic features of beaver in boreal regions. Beaver ponds can cover a large portion of the landscape due to the fairly low relief and drown existing vegetation. They cause an elevation of the local water table, which influences soil nutrient cycling and vegetation composition. In-filling of ponds with sediment over time leads to the development of unique patches that undergo different successional processes after beaver abandonment than the surrounding landscape. Beaver ponds dug out in peatlands may also affect local hydrogeomorphic processes less than ponds formed in river channels. However, peatlands beaver ponds probably have a much longer legacy on the landscape as there is no documentation to suggest that they fill in with sediment over time and eventually become meadows.

In other parts of North America where landscapes are not as flat, the effects of beaver can extend beyond the ponds. The ponds may be quite small compared with the overall effects of beaver dams on landscape processes. In-channel beaver dams can divert a large portion of the river discharge out of the channel and across valleys, which beaver can subsequently re-direct by building a network of off-channel dams and canals. This may connect oxbows or abandoned channels to the main river and allow beaver to selectively forage vegetation far from the river channel. It also allows sediment to accumulate on floodplains and terraces, which create spatially heterogeneous landforms. The plant community structure in valleys influenced by beaver is thus highly variable and establishes multiple successional trajectories. As the beaver-created landforms are often disconnected from the river when the in-channel dam breaches, the legacy of beaver on these landscapes may be quite long.

4.8 References

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